Carl Chun

THE CEPHALOPODA

PART I: OEGOPSIDA
PART II: MYOPSIDA, OCTOPODA

TEXT

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THE CEPHALOPODA

GERMAN DEEPSEA EXPEDITION 1898–1899. VOL. XVIII

SCIENTIFIC RESULTS OF THE GERMAN DEEPSEA EXPEDITION
ON BOARD THE STEAMSHIP "VALDIVIA" 1898–1899

Volume Eighteen

UNDER THE AUSPICES OF THE GERMAN MINISTRY OF THE INTERIOR

Supervised by CARL CHUN, Director of the Expedition
Professor of Zoology, Leipzig.
After 1914 continued by
AUGUST BRAUER
Professor of Zoology, Berlin

CARL CHUN

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Since the study of the Cephalopoda is a very specialized field with a unique and specific terminology and phraseology, it was necessary to edit the translation in a technical sense to insure that as accurate and meaningful a representation of Chun's original work as possible would be achieved. We hope to have accomplished this responsibility.

Clyde F. E. Roper and Ingrid H. Roper
Technical Editors

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Carl Chun

THE CEPHALOPODA

PART I: OEGOPSIDA

TEXT

GERMAN DEEPSEA EXPEDITION 1898–1899. VOL. XVIII, PART I

WISSENSCHAFTLICHE ERGEBNISSE

DER

DEUTSCHEN TIEFSEE-EXPEDITION

AUF DEM DAMPFER „VALDIVIA" 1898-1899

IM AUFTRAGE DES REICHSAMTES DES INNERN

HERAUSGEGEBEN VON

CARL CHUN

PROFESSOR DER ZOOLOGIE IN LEIPZIG

LEITER DER EXPEDITION

ACHTZEHNTER BAND

CARL CHUN

DIE CEPHALOPODEN

I. TEIL: OEGOPSIDA

MIT EINEM ATLAS VON 61 TAFELN UND 32 ABBILDUNGEN IM TEXT

TEXT

JENA

VERLAG VON GUSTAV FISCHER

1910

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General Part

COMPARATIVE REVIEW OF ORGANIZATION

Oegopsida d'Orbigny, 1839

Chondrophora Gray, 1849 p.p.

Decapodes pelagici Steenstrup, 1861

The Decapoda Oegopsida are all inhabitants of the open sea and avoid life on the bottom—be it in the deep sea or in shallow water. Compared to the Myopsida and Octopoda, they form the majority of the pelagic Cephalopoda. Since this volume deals with the Oegopsida of the deep sea, it should be stressed that little is known of their vertical distribution, particularly about the depths at which the species described in this volume normally occur. They are excellent swimmers and easily avoid nets, including closing nets. Only a few larvae have been caught in closing nets at depths to 1,500 m (Plate XXIX, Figures 12, 13), but their identities could not be determined with certainty. Mature animals were never caught in these nets. An exact determination of the vertical distribution is rarely possible by other methods. Thus, we found partly digested remains of *Abraliopsis* in the stomach of *Colocon-ger raniceps* Alc., a benthic fish which was dredged at a depth of 628 m at Station 265.

Determination of the vertical distribution is also made difficult by the rarity of the material. Every species caught in the large vertical nets or accidentally caught while the trawl was being hauled up gave us great satisfaction, since we realized another specimen might not be caught during the voyage.

Our views on the mode of life of the deep-sea pelagic forms are not contradicted by the isolated specimens caught at the surface—at night or under other circumstances. These were either dead or exhausted specimens the behavior of which suggest exposure to unusual condition. Joubin (1905, No. 33, pp. 1–2) reported that numerous specimens of *Leachia cyclura* were caught on the surface during 2 days of a voyage of the *Prince of Monaco* between the Canaries and the Azores in August 1904.
4 The animals, which died within a few hours of captivity, proved to be females that had already spawned. In other cases, mature males of deep-sea species were found drifting at the surface, probably having risen in pursuit of the females. I have in hand a large male of *Calliteuthis ocellata*, found drifting by fishermen in Sagami Bay, Japan, and sent to Professor Doflein. Such deep-sea forms reach the surface in a better condition when the temperature differences are not too great. This applies particularly to

Mediterranean species carried by deep currents to the surface. The occurrence of such specimens in the port of Messina has long attracted the attention of biologists.

Phylogenetically the Oegopsida are the older and primitive Decapoda. This was recognized also by earlier observers, including Brock (1880, p. 56), in spite of inadequate anatomical knowledge. Moreover, the systematic position of some Cranchiidae was incorrectly determined, and the controversy on the question whether *Spirula* belongs to the Oegopsida or to the Myopsida continues today. The fact that the Oegopsida are the primitive and phylogenetically more ancient Decapoda has as yet not gained due recognition among scientists. I have stressed this view ever since I took up the study of Cephalopoda and shall attempt to prove it in the following review of the morphology of the Oegopsida. Jatta (1896) and Pfeffer (1900) have already published short, comparative descriptions of Oegopsida, but they emphasized solely the important systematic characters. I shall thus discuss only those organ systems in greater detail on which our knowledge has increased in recent years, either due to the collection of new material or due to dissection of interesting, and in some cases new, species.

EXTERNAL CHARACTERS

Forms of the Body

The **form** of Oegopsida is largely determined by the mantle and is usually shaped like a cone or a goblet, sometimes like a spindle or bolt. Oegopsida are usually slender and move rapidly through the water, cutting it like an arrow, and indeed sometimes looking like one. This applies particularly to the characteristic genus of Cranchiidae, *Toxeuma* (Plate LVIII) and also to *Taonius*, *Taonidium* and *Doratopsis*. Other Oegopsida, however, have a plump, sac- or barrel-shaped body, with small arms and fins (*Teuthowenia* and *Bathothauma*) or large arms with wide, sometimes sail-like margins (*Histioteuthis* and *Chiroteuthis*). The form of the body may vary markedly in the same family. Thus, the Cranchiidae show all the forms mentioned above.

The form of the body changes considerably also during postembryonic development. Plate XII shows the postembryonic development of *Pterygioteuthis*. The young forms are barrel-shaped and have a rounded posterior end from which project small fins. The animal gradually becomes goblet-shaped as the posterior end becomes more pointed and finally projects as a spine beyond the fins.

The **consistency** of the body is usually tough and muscular, rarely membranous. The deep-sea forms often have a tendency to develop a gelatinous connective tissue which may either be restricted to certain areas of the body, or extend over the entire body. Thus, *Enoploteuthis leptura* (Plate XI, Figure 5) has a gelatinous posterior end, and many Cranchiidae have a gelatinous head and eyestalks. A gelatinous structure of the whole body is present to a varying degree in *Octopodoteuthis* (*Veranya*), *Benthoteuthis*, *Ctenopteryx*, *Chaunoteuthis*, and in the families Histioteuthidae and Chiroteuthidae.

The body is always **differentiated** into four clearly defined regions: mantle, funnel, head, and arm region.

Head

The **head** part is usually comprised of a neck which extends from the posterior margin of the eyes to the insertion of the musculus collaris.

The neck is unusually long and cylindrical in the genus *Chiroteuthis* and its juvenile form, described as *Doratopsis*. The juvenile forms of *Brachioteuthis* (*Tracheloteuthis*), described previously under various names, also have a long, thin neck (Plate XXIX, Figures 9, 10) which gives them a bizarre appearance, especially the younger stages. The anterior part of the head may also be markedly lengthened, forming what I name a "head pillar". This is especially characteristic for *Doratopsis* and the stalk-eyed Cranchiidae *Teuthowenia*, *Euzygaena*, *Crystalloteuthis*, *Corynomma*, *Sandalops*, *Toxeuma* and *Bathothauma*.

In some families, the neck forms folds, generally in two systems: transverse and longitudinal folds. These formations have been described in detail by earlier workers, and recently by Jatta and Pfeffer, and will therefore not be discussed here.

Mantle

The **mantle** determines the form of the body. It may be conical or goblet-shaped, sometimes spindle-shaped because it is inflated in the middle; sac- or barrel-shaped mantles also occur. In the latter case, the body has a rounded posterior end, whereas it otherwise ends in a more or less long point. The outer and inner sides of the mantle are lined with epithelium attached with connective tissue. The connective tissue forms a thin layer on the inner side, while it is thick, and often consists of several layers, on the outer side. Chromatophores are embedded in the thin layer of connective tissue (cutis), often in several superimposed layers.

The greater part of the mantle is comprised of smooth musculature consisting mainly of strong circular fibers crossed perpendicularly by radiating fibers. The nuclei of the radial fibers are embedded in widened lamellae in the middle of the mantle, from which the fibers radiate toward the periphery.

6 The free mantle margin projects more or less distinctly at three points: a dorsomedian and two ventrolateral points. These projections are named mantle corners; the depression containing the funnel is usually situated between the ventral mantle corners.

The surface of the mantle is usually smooth, and in some Cranchiidae covered with tubercles which consist of cartilage. These tubercles may be distributed uniformly all over the surface, as in *Cranchia scabra*, or confined to the strips of concrescence on the dorsomedian line which will be described below. In *Crystalloteuthis* the tubercles are antler-shaped formations on the mantle corners.

There are in addition 3 cartilaginous stripes on the inner side of the mantle, opposite the neck and funnel cartilage, which will be described in connection with the latter.

Joubin (1895, 1900) described a cephalopod found in the stomach of a whale and named it *Lepidoteuthis* because the mantle was apparently covered with scales. They form a polyhedral pattern, like the scales of ganoids, and consist of fibrous connective tissue. In my opinion, however, these are not true scales, but peculiar structures of the deeper layers of the cutis which project like pillars toward the surface. They are covered with epithelium and the outer layers of connective tissue and become more distinct only if the superficial layers are destroyed by the action of gastric juice. I consider the genus *Lepidoteuthis* as identical with *Chaunoteuthis*, described by Appellöf (1891), of which I have a well-preserved specimen in which these structures can be recognized indistinctly beneath the smooth skin.

Fins are present in all Oegopsida. They are situated dorsally on the posterior end of the body and are rarely widely separated (*Bathothauma*). Their bases are usually contiguous posteriorly and diverge anteriorly. Young larvae have small, almost circular fins. Such small fins are present throughout life in *Benthoteuthis* and some Cranchiidae, e.g., *Teuthowenia* and *Bathothauma*. Usually, however, the fins are elongated anteriorly and either widely diverge, attached to the lateral parts of the body, or almost fuse in the dorsal midline (*Chiroteuthis*, *Histioteuthis*). In the genera *Ancistroteuthis*, *Thysanoteuthis* and *Ctenopteryx*, the fins grow to the anterior mantle margin. The fins consist of a regular pattern of radiating muscular bundles inserted in a fin cartilage; in *Ctenopteryx* the fins are pectinate, more widely spaced and resemble a comb.

The delicate membranous margins without muscles which surround the posterior end of the body in *Doratopsis* and *Chiroteuthis imperator* have to be distinguished from true fins. In *Grimalditeuthis*, the margins are fused into a transparent disk behind the true fin and are completely separated from it.

Funnel

Jatta and Pfeffer have described the funnel in detail, but some important structures have never been described and deserve attention.

7 The **funnel** is a muscular tube which projects freely from the margin of the mantle between the ventral mantle corners, and its dorsal side is situated in a depression on the head. Sometimes this depression is absent, and in the Ommatostrephidae its anterior margin bears a system of folds. A funnel valve with a semicircular, free anterior margin is situated on the dorsal inner surface of the funnel, close to the opening. In the Cranchiidae I have never found such a valve, but in all other Oegopsida I found it constant.

The inner surface of the funnel contains a mucous gland—the "**funnel organ**". It was discovered by H. Müller (1853, p. 339), who proved its presence in the Oegopsida and also in the Myopsida and Octopoda. This gland was later described by Verrill (1881, p. 413) in *Desmoteuthis tenera*, and Laurie (1889, p. 97) therefore named it "Verrill's organ", having had no knowledge of Müller's observations. A more detailed description of this organ was given by Jatta (1893, p. 15; 1896, pp. 21–23). Whether this gland is homologous to the pedal gland of other molluscs, as I assume it to be, will have to be decided on the basis of a more detailed study of its structure and development.

The funnel organ of Oegopsida consists of 3 parts: a single dorsal and two paired ventral parts. The dorsal part is bifid or heart-shaped: in the Cranchiidae it bears tongue-shaped appendages. The vena cava reaches the ventral wall directly behind it. The paired ventral parts are usually oval.

Three pairs of muscles are closely connected with the funnel. From the lateral walls of the funnel there radiates the **musculus collaris,** which forms a collar extending to the neck cartilage; its insertion on the body marks the boundary between head and neck. This muscle forms a valve which prevents escape of respiratory water through the mantle margin during the contractions of the strong circular musculature of the mantle, forcing the water to pass through the funnel opening. All Oegopsida have a well-developed musculus collaris. This applies particularly to the slender arrow-shaped forms, which move by the forceful ejection of the respiratory water.

The **funnel adductors** show important systematic characters. They usually form pairs, but often are fused into a broad muscular plate. These muscles reach the funnel wall lateral to the head. The funnel adductors of the Chiroteuthidae and Cranchiidae are not recognizable from the outside, but in the Chiroteuthidae they are visible through the gelatinous skin as whitish bands.

Cutting open the mantle cavity reveals large muscles which radiate into the dorsolateral walls of the

funnel. These **musculi depressores infundibuli** are usually strongly developed; they taper posteriorly and end behind the branchial hearts, near the dorsal wall of the mantle (Plate XXVI, Figure 1). In the Chiroteuthidae and Tracheloteuthidae (Figure 1), they form lamellae which also taper near the base of the gills (Plate XXXVI, Figures 1; 2; Plate XLII and XLIII, Figure 1).

The **funnel cartilages**, situated on the lateral posteroventral margin of the funnel, are of charac-
8 teristic form in each family; they are fitted into the mantle cartilage and form a closure apparatus. The musculus collaris is inserted on the neck in a flat, oblong cartilage the counterpart of which is the dorsal mantle cartilage. In some genera (*Symplectoteuthis*, *Grimalditeuthis*), the funnel cartilages are so firmly fused that the mantle margin is connected with the funnel at two points. This is especially the case in the Cranchiidae, in which the two neck cartilages, too, are fused (Plate XLIX, Figure 3).

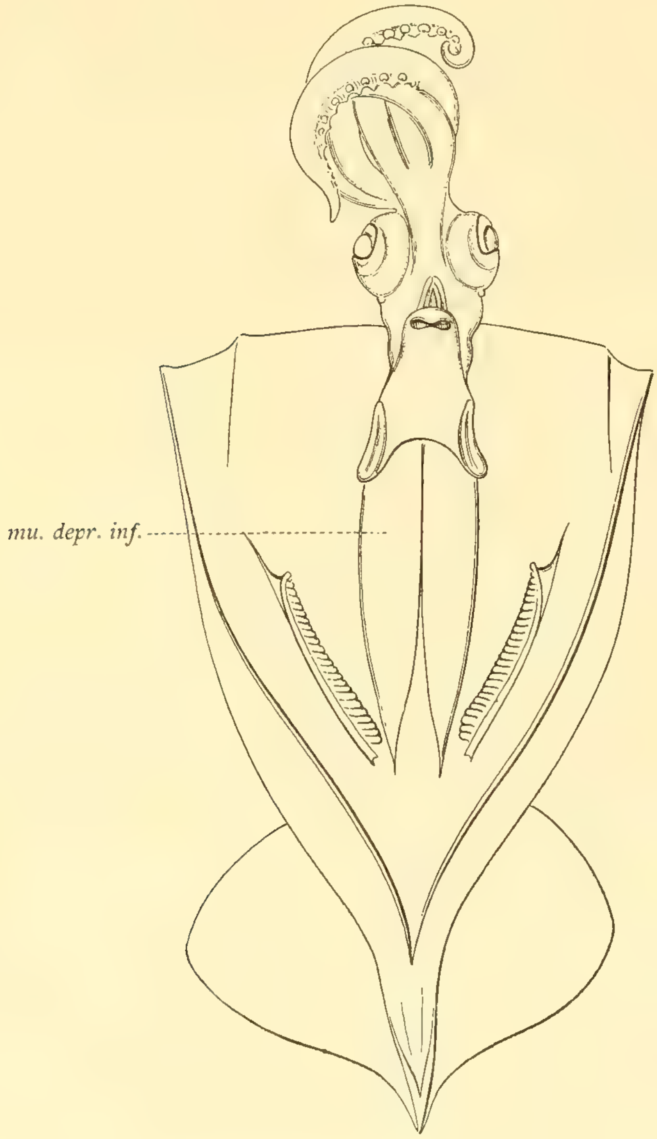

FIGURE 1. *Brachioteuthis riisei* STEENSTR.

Visceral sac removed and gills cut off at the base; *mu. depr. inf.* band-shaped funnel depressors.

Funnel Apparatus of the Cranchiidae

The fusion between mantle and funnel at 3 points has been considered to be the main character of the Cranchiidae, but it was overlooked that this condition is associated with certain modifications of the whole funnel apparatus, which are, in my opinion, much more important. These modifications are not restricted to the funnel proper, but also affect the musculus collaris and the depressor muscles. Having hardly ever been dealt with, these conditions will be discussed in greater detail later, but the principle of those peculiar modifications is briefly described here.

The músculus collaris does not form a circular band but splits into two lobes at its projection into the mantle cavity. The split ensues by its being parted both in the median dorsal line and at the point of insertion in the funnel. The two parts of the musculus collaris do not project freely into the mantle cavity but are fused with the inner surface of the mantle at their lateral margins. Their concave posterior margin remains free, so that the musculus collaris is transformed into two large valves which prevent escape of water through the mantle margin.

A similar fusion takes place on the funnel itself. The posterior half of the funnel, which is covered by the mantle, is divided on both sides to the fused ventral corners of the mantle, forming a
9 ventral funnel lobe and a separate dorsal part. The lateral margins of the ventral lobe are fused with the inner surface of the mantle, while the projecting ventral posterior margin remains free, converting the whole part into a pocket valve.

All Cranchiidae have thus 3 pairs of strips of attachment which diverge posteriorly at an acute angle and delimit 3 valves. One pair is situated dorsally and belongs to the dorsal margin of the musculus collaris; the two lateral pairs originate on the lateral walls of the funnel and delimit dorsally the m. collaris and ventrally that part of the funnel which is covered by the mantle.

Another concrescence results from a modification of the m. depressor infundibuli. As stated above, this muscle is bandshaped in the Chiroteuthidae and Tracheloteuthidae. It is even wider in the Cranchiidae, in which its free margins are fused with the lateral wall of the mantle, so that the whole muscle forms a broad band that divides the mantle cavity anterior to the gills into two paired dorsal parts and a single ventral part. The homology of this muscular band to the musculus depressor infundibuli is evident from its topographic relationship. As in the other Oegopsida, in the Cranchiidae this muscle appears at first as a narrow band behind the branchial hearts. It widens rapidly and is attached at one end to the ventral wall, extends to the dorsal side of the funnel, surrounds the anterior margin of the gills in an elegant curve and is then attached to the lateral wall of the mantle. Anteriorly the muscle reaches the point of fusion of the ventral margin of the m. collaris.

Furthermore, the gill ligament reaches the depressors at its anterior margin and passes into their posterior margin. The two parts of the mantle cavity formed by the broad depressor muscle communicate with the larger, unpaired part by two broad openings, which I call spiracula. Opening of the mantle cavity readily shows these openings as two wide slits, delimited by the curved free posterior margin of the depressors.

This rather complicated condition will be illustrated by the following partly diagrammatic figures based on the structure in *Cranchia.*

Figure 2 shows a ventral view of *Cranchia.* The ventral wall of the funnel (*inf. v.*) with its lateral strips of attachment and its concave free posterior margin are visible through the mantle. The lobes of the m. collaris (*coll.*), which are also converted into pocket valves, are visible laterally with their ventral strips of attachment.

The two muscular bands formed by a modification of the depressors (*mu. depr. inf.*) are visible

in their entire width. They begin at the ventral wall, are fused with the lateral margins of the mantle and extend together anteriorly with the ventral attachment of the collaris. Their curved posterior margin is situated anterior to the gills the suspensorium (*susp.*) of which is fused anteriorly with the depressors. The spiracula (*spirac.*) are delimited along the whole gill by the curved posterior margin of the depressors.

Figure 3 shows these conditions in lateral view. It shows the entire right pocket valve of the m.

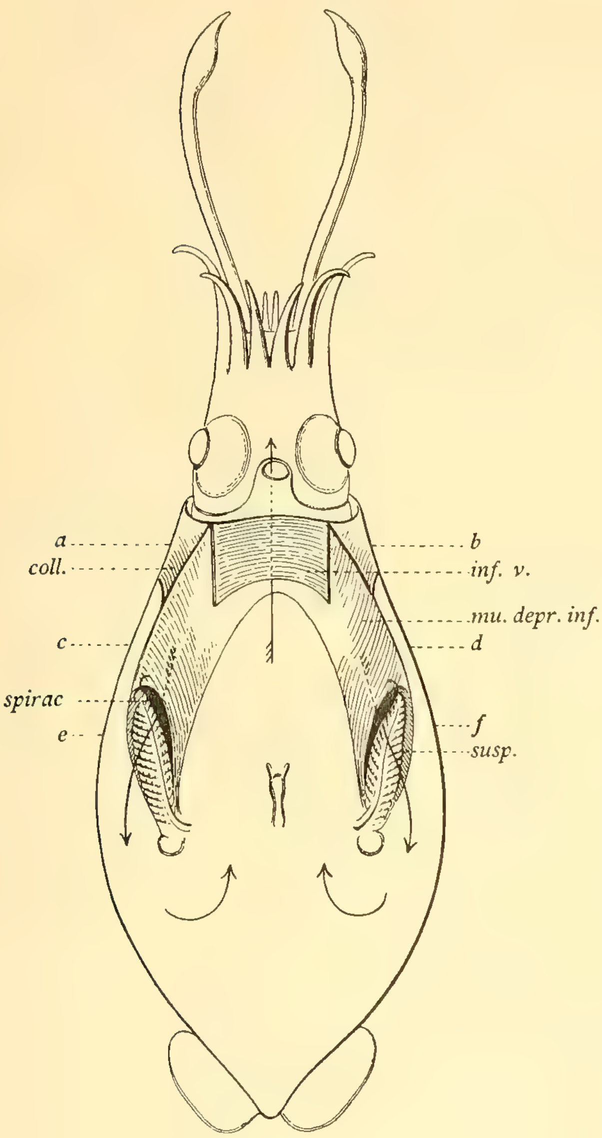

FIGURE 2. *Cranchia*, ventral;

a . . . b level of section in Figure 4;
c . . . d level of section in Figure 5;
e . . . f level of section in Figure 6.

coll. musculus collaris; *inf. v.* ventral wall of funnel; *mu. depr. inf.* funnel depressors; *spirac.* spiraculum; *susp.* suspensorium of gill. (Arrows indicate direction of water current).

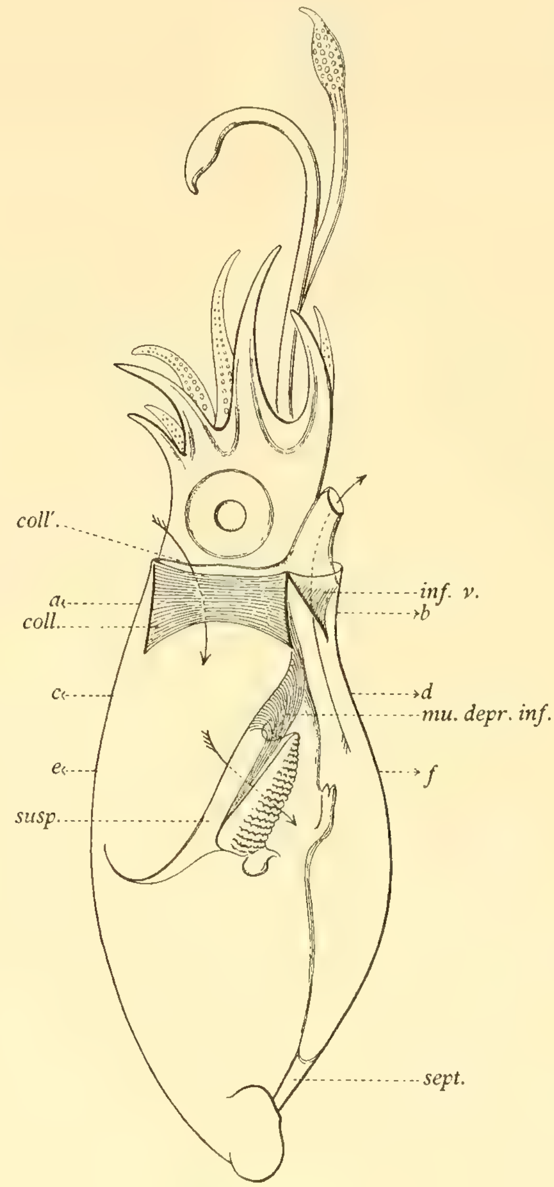

FIGURE 3. *Cranchia*, right side:

a . . . b level of section in Figure 4;
c . . . d level of section in Figure 5;
e . . . f level of section in Figure 6.

coll'. attachment of the m. collaris on the head; *coll.* lateral lobe of collaris fused with the mantle; *mu. depr. inf.* funnel depressor; *sept.* mantle septum; *susp.* suspensorium of gill. (Arrows indicate direction of water current).

10 collaris (*coll.*) and the corresponding half of the ventral funnel valve (*inf. v.*). The right musculus depressor infundibuli appears markedly shortened in this view; its margin is fused with the mantle and connected with the attachment of the branchial suspensorium (*susp.*), which extends far posteriorly and dorsally.

11 These apparently complicated conditions are illustrated by a series of slightly diagrammatic cross sections of a young *Cranchia.*

The section in Figure 4 passes through the collaris and the posterior part of the funnel in the middle of the drawing (level *a . . . b*). The visceral sac, cut at the level of the statocysts (*stat.*), is visible in the middle of the drawing; the gladius (*glad.*) is visible dorsally in cross section. The visceral sac adheres to the dorsal posterior wall of the funnel; this wall ends laterally in the depressors (*mu. depr. inf.*); the ventral wall of the funnel (*inf. v.*) is completely separate from its dorsal wall; it is transformed into a

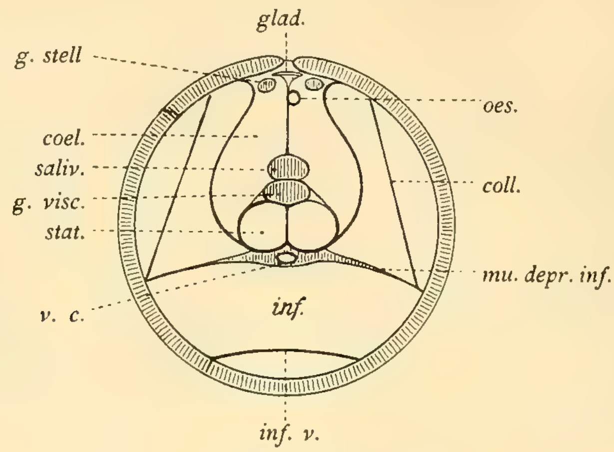

FIGURE 4

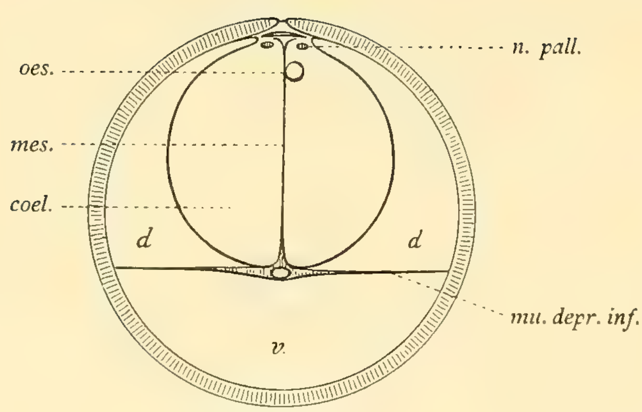

FIGURE 5

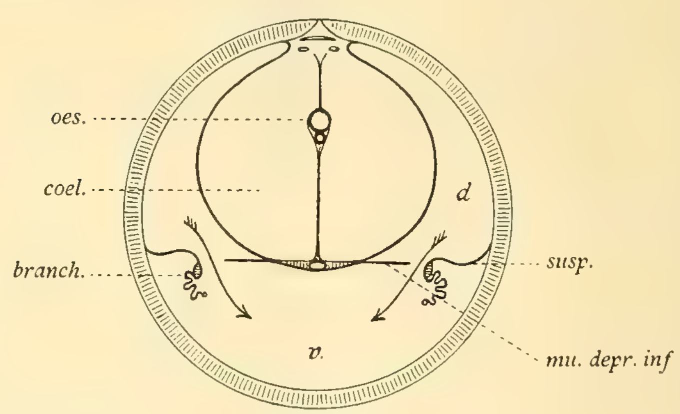

FIGURE 6

Semi- or diagrammatic cross sections of *Cranchia*:

Figure 4—Cross section at level *a . . . b* of Figures 1 and 2;
Figure 5—Cross section at level *c . . . d* of Figures 1 and 2;
Figure 6—Cross section at level *e . . . f* of Figures 1 and 2.

branch. gill; *coel.* coelom; *coll.* musculus collaris; *d* dorsal parts of mantle cavity; *glad.* gladius; *g. stell.* stellate ganglion; *g. visc.* visceral ganglion; *mes.* mesenterium; *inf.* funnel; *inf. v.* ventral wall of funnel; *mu. depr. inf.* funnel depressors; *n. pall.* pallial nerve; *oes.* esophagus; *saliv.* posterior salivary gland; *susp.* suspensorium of gill; *v.* ventral part of mantle cavity; *v. c.* vena cava. (Arrows in Figure 6 show the direction of the flow of water through the spiracula).

pocket valve and fused laterally with the mantle. The two lobes of the collaris (*coll.*) are connected obliquely with the point of fusion of the depressors with the mantle.

The section in Figure 5 passes behind the funnel and the collaris (level *c . . . d*). Here a median septum (*mes.*) divides the coelom (*coel.*) of the visceral sac into two separate halves. At the dorsal margin of the septum one sees the cross section of the esophagus, at its ventral margin —the vena cava. The depressors are cut at their full width at this level and divide the mantle cavity into two lateral dorsal parts (*d.d.*) and a single ventral part (*v.*).

The section in Figure 6 (level *e . . . f*) passes through the spiraculum, which is the only communication between the dorsal (*d.d.*) and ventral (*v.*) parts of the mantle cavity, as shown by the arrows. The gills (*branch.*) border the spiracula on both sides, and their suspensoria (*susp.*) pass along the narrowed depressors.

12 Physiologically, the whole modification mechanism channels the flow respiratory water, which is also used for locomotion, more efficiently than is the case in the other Oegopsida. During expansion (diastole) of the mantle, water enters the two dorsal mantle sacs through the lateral slits of the mantle (Figure 3). Contraction (systole) of the mantle musculature expels the water with great force through the spiracula into the ventral mantle cavity; at the same time, the m. collaris, converted into a pair of valves, prevents escape of water through the mantle slit more efficiently than in other Cephalopoda. The gills are situated in front of the spiracula, and thus receive a direct supply of fresh water. Toward the end of the systole, the water is expelled through the funnel, its recoil propelling the animal with its posterior end foremost. The ventral wall of the funnel is transformed into a valve which prevents escape of water through the ventral mantle slit more efficiently than in other Cephalopoda. The gills with their suspensoria are pressed against the spiracula, which prevents escape of water from the unpaired ventral mantle cavity through the spiracula. There are thus two dorsal currents which are directed posteriorly and a ventral current which passes anteriorly through the funnel. This sharp separation of water currents, together with the mechanisms which prevent escape of water through the mantle slit is, in my opinion, the most important characteristic of the Cranchiidae.

Since these structures are unique among the Cephalopoda, and in view of the other aberrant characters of the Cranchiidae, I consider it justified to separate the Cranchiidae from all other Oegopsida, and I therefore divide the order Oegopsida into 2 suborders, as follows:

Oegopsida libera.	Funnel apparatus free. Funnel valve present.
Oegopsida consuta.	Funnel apparatus (ventral funnel wall, m. collaris and depressors) fused with mantle. Funnel valve absent.

Arm apparatus

All Oegopsida have 8 arms and 2 tentacles. If their number is reduced in mature animals, this is due to secondary reduction or else discard of previously present arms or tentacles.

The **arms** are usually fleshy, rarely gelatinous (Veranyidae, Bathyteuthidae, Histioteuthidae, Chiroteuthidae). Compared to the body, they are either shorter (Cranchiidae), as long, or longer and sometimes very large, particularly in the Histioteuthidae and Chiroteuthidae. For systematic de-

scriptions, it is customary to number the arm pairs, beginning from the dorsal arms as the first pair; thus, the dorsolateral, ventrolateral and ventral arms are designated respectively as the 2nd, 3rd and 4th arms. Since the 8 arms usually differ in length, their relative length is described using a formula in
13 which the arms are listed in the order of decreasing length: i.e., the longest arms are named first. In the Chiroteuthidae, for example, where the ventral arms are markedly longer than the other pairs, while the dorsal arms are the shortest, the arm formula of the family is: 4, 3, 2, 1.

The arms are either rounded or have an angular cross section. In the latter case, they have 4 surfaces: an outer surface, an inner surface with suckers or hooks, and 2 lateral surfaces of which the one facing the dorsal arms is considered as dorsal and that facing the ventral arms as ventral. The same terminology is used for the rows of suckers and the membranes described below.

The detailed structure of the arms, with reference to the arrangement of their musculature and innervation, has been studied by Colasanti (1876) and recently by Guerin (1908), who investigated the arms of the Myopsida and Octopoda with particular thoroughness, but a comparative description for the Oegopsida is still lacking.

The **membranes of the arms** have been described in detail. However, a brief outline of these formations is desirable.

The term "**swimming keel**" is used for the single membrane on the outer surface of the arms. Some swimming keels extend along the whole arm; others are restricted to its distal part. They may be keel- or crescent-shaped, with a marked widening in the middle. They are sometimes situated on the boundary between the outer and lateral surfaces of the arm, e.g., on the ventral arms of *Chiroteuthis*.

The "**protective membranes**" are paired membranes along the rows of suckers or hooks; they bear transverse muscular bridges which are cirrate or conical. Since the protective membranes are often very delicate, the skin between the muscular bridges is easily torn or is lost, so that the arm appears to have a row of lateral cirri (*Cirrobrachium* Hoyle). The muscular bridges constantly alternate with the adjacent suckers or hooks, so that the ventral and dorsal muscular bridges of the same arm alternate. The protective membranes are sometimes asymmetrical, inasmuch as either the dorsal or the ventral membrane may be more strongly developed. Some Ommatostrephidae (*Stenoteuthis*) have very wide protective membranes.

In most genera, the protective membranes disappear toward the base of the arm; in some, however, they widen at the base to sail-like formations. Such a sail-shaped widenong of the protective membranes is present, for example, between the 1st and 2nd arms of *Cranchia scabra* and between the 1st, 2nd and 3rd arms of *Pterygioteuthis*.

In the adult *Histioteuthis* these webs are enormously developed. The "sail" of this form, the morphological interpretation of which was not given by earlier authors, developed from the protective membranes, as I proved in a brief communication (1906, p. 744). As the instructive illustrations of Férussac and Vérany show, this "sail" connects only the 1st, 2nd and 3rd arms (Plate XXI). The tentacles and the ventral arms are situated outside the "sail". However, the ventral arms are connected with the "sail" by their ventral protective membranes which are lengthened toward the base and reach the ventral median surface of the "sail" on each side.

14 Other membranes, independent of the swimming and protective membranes, connect the outer surfaces of the bases of the arms; I call these "**outer membranes**". The outer membranes are present constantly between the bases of the 3rd and 4th arms surrounding the tentacles. They often pass here into the swimming membranes of the ventral arms, and it is doubtful whether they belong to the swimming membranes. If they are present between the other arms, however, the outer membranes are independent of the swimming membranes. In *Histioteuthis*, the outer membranes are present between all arms, forming

pockets between the adjacent arms and between the large "sail" of the protective membranes and the outer membranes.

The **suckers and hooks** are of great systematic importance. They form an alternating biserial pattern on the inner surface of the arms. There are rarely 4 rows, as in *Gonatus*. In the following descriptions I shall demonstrate many times that the juvenile forms of all hook-bearing genera originally had only suckers.

The armtips of *Octopodoteuthis* and *Grimalditeuthis* end in terminal knobs, the significance of which is not known. There are 3 such knobs on the ventral arms of *Abraliopsis;* in *Histioteuthis* the distal outer surface of the armtips bears oblong glandular pads.

The **postembryonic development of the arms** shows that the dorsal arms develop before the others. The youngest larvae at hatching often have only the 1st and 2nd arms. Then the 3rd, and finally the 4th arms develop. This sequence applies especially to the larvae of Enoploteuthidae, Ommatostrephidae, Onychoteuthidae and Cranchiidae.

The **tentacles** of the youngest larvae closely resemble arms. The youngest larvae of Onychoteuthidae (Plate XXIII, Figures 2, 4, 6) have only 6 arms and the ventral pair of arms develops into tentacles. The tentacles attain their typical form in the later stages, after the formation of the short stumps of the 3rd and 4th arms. The tentacles become differentiated into a stalk and a club which can be divided into a proximal carpal part and a distal hand part. *Octopodoteuthis* has very short tentacles which later disappear. Tentacles have not been demonstrated in the genera *Chaunoteuthis*, *Leachia* and *Taonius*. However, the existence of short stumps between the 3rd and 4th arms of these forms suggests that tentacles were originally present but later disappeared. The tentacles are usually longer than the arms and they are extremely long in the Cranchiidae and Chiroteuthidae.

In contrast to the Myopsida, the tentacles are not retracted into pockets. Only in the pterygiomorphous Enoploteuthidae is the coiled base of the tentacles retracted into a pocket between the eyes.

15 The **stalk of the tentacle** is rounded or angular, with a more or less flattened inner surface. A spindle-shaped swelling at the base is present in *Pterygioteuthis* and *Pyroteuthis*.

Because of its systematic importance, the **tentacular club** has been described in detail by all authors. The tip of the club is often curved dorsally like the horn of a chamois. It usually bears a single swimming membrane which is displaced dorsally because of the curvature of the tip. The protective membranes are present as they are on the arms but are often asymmetrically developed—the ventral membranes being more strongly developed than the dorsal ones.

The **suckers of the tentacles** are arranged in oblique rows of four; more than 4 rows are present in the Tracheloteuthidae, Bathyteuthidae, Histioteuthidae, in *Mastigoteuthis*, *Gonatus* and on the tip of the club of *Illex*. The suckers of the two median rows often show a tendency to become enlarged at the expense of those of the marginal rows. If the suckers convert into hooks—as they do in the Enoploteuthidae, Onychoteuthidae, *Gonatus* and *Taonidium*—the conversion takes place only in the course of postembryonic development. Usually only a few suckers develop into hooks, and even if a greater number of suckers is transformed into hooks, small suckers persist on the tip of the club.

Pfeffer divides the hand part of the club into two parts, a proximal, or true hand part, and a distal part. Since, however, these two parts usually merge imperceptibly into each other, I refer to a proximal and a distal hand part only in cases where such a differentiation has taken place.

The hand part of the club of most Oegopsida is distinguished from a proximal **carpal part** which serves for mutual attachment of the two tentacles by suction. The carpal part consists always of suckers and of knoblike thickenings between them onto which fit the openings of the suckers on the opposite tentacle. As Steenstrup has shown, the arrangement of the adhesive knobs corresponds exactly to that

of the suckers on the opposite tentacle. In young specimens it seems that these knobs have indeed come to be formed by this very suction of the opposite tentacle.

The carpal part either merges smoothly into the hand part (Cranchiidae, Tracheloteuthidae) or is sharply differentiated from the latter (Enoploteuthidae, Onychoteuthidae). In *Gonatus*, in the Histioteuthidae, Tracheloteuthidae, Ommatostrephidae and, especially, in the Cranchiidae, the carpal part extends on a great part of the stalk. In the latter case, the carpal part bears two rows of suckers which alternate with knobs; as will be shown later, this condition develops from a stretched quadriserial pattern.

A special character of *Chiroteuthis* is the presence of knoblike thickenings on the outer side of the tentacle stalk and of a large knob on the tip of the club. Pfeffer (1900, p. 183) considers these knobs to be modified suckers, while Joubin (1893) interprets them as catching organs which capture small pelagic orgamisms by means of protoplasmic appendages. My studies show that these are glandular knobs which apparently secrete a poisonous substance.

As regards the **development of the tentacles,** it has already been mentioned that they at first
16 closely resemble the arms and bear suckers to the base. They apparently develop earlier than the arms and in any case exceed the latter in further development.

For the morphological equivalence of the tentacles and arms I find evidence not only in the similarity of their early "anlagen" but also in the arrangement of the suckers. My examination of the youngest larvae of Enoploteuthidae and Onychoteuthidae showed clearly that the earliest suckers of the tentacles are arranged in 2 alternating rows, exactly as on the arms, and not in 4 rows (Plate VII, Figures 10, 13, 25; Plate XIII, Figure 12; Plate XXIII, Figure 2). It is this condition that persists in the about-to-be-discarded tentacles of *Octopodoteuthis* (*Veranya*) (Plate XVII). Since no interpolation of suckers ever takes place between already existing suckers (new suckers always appear at the distal end of the arms and of the tentacle club, where they are arranged in rows of four), it has to be assumed that the biserial suckers of the tentacles serve mainly for the formation of the carpal part. This will be proved later for the larvae of *Teleoteuthis*.

A very aberrant condition is present on the tentacles of larvae of Ommatostrephidae (Plate XXVIII). As I have shown (1903), these tentacles are fused into a thick, proboscis-like process which has a few apical suckers. Only later a separation takes place, at the base of the fused tentacles, gradually setting the two tentacles entirely apart. I named these larvae *Rhynchoteuthis*; Hoyle (1904) and Pfeffer (1908) described stages in which the tentacles are almost completely separated, except at the clubs.

Hectocotylization

In his famous work *Hectocotyldannelsen* (1856), Steenstrup described the modification of one of the arms into a copulatory organ only for Octopoda and Myopsida. Only in the wake of this work, cases of hectocotylization were discovered also in the Oegopsida. Until recently, knowledge in this field was rather fragmentary, since hectocotylization was known in only two families: the Enoploteuthidae and Ommatostrephidae. I found hectocotylization also in the Histioteuthidae and Cranchiidae.

In all cases that had been known, hectocotylization in the Oegopsida involves one of the ventral arms. It is therefore peculiar that in the Histioteuthidae, alone of all the cephalopods, the two dorsal arms are affected by hectocotylization (Chun, 1906). It is hard to decide whether this unique condition is a primitive one. It is, at any rate, noteworthy that in the genus *Calliteuthis* (Histioteuthidae) I found double male genital ducts.

HOYLE (1907, p. 5) has supplied a list of all known cases of hectocotylization. It seems desirable, however, to present a special list of hectocotylization in the Oegopsida, with brief notes on the affected arms and the authors:

17 Enoploteuthidae

Abralia: Left ventral arm; without hooks at the tip and with 2 glandular ridges. CLAUS, 1858.

Abraliopsis: Left ventral arm; ventral protective margin strongly developed. HOYLE, 1904, Plate X, Figure 1.

Pterygioteuthis: Left ventral arm; suckers and hooks absent; middle part with 2 large glandular pads, between which is situated a toothed plate with a system of lamellae. CHUN, 1904, 1908, Plate XV, Figures 1, 2, 3.

Pyroteuthis: Right ventral arm; distal area covered with a ventral glandular lobe which separates the hooks. CLAUS, 1858, Plate XI, Figures 2, 3.

Ommatostrephidae

Ommatostrephes: Left ventral arm; suckers at the tip absent, their basal pad enlarged like a papilla. Protective membranes large, thick (this modification is stated to be present in all genera of Ommatostrephidae). PFEFFER, 1900.

Todaropsis: Both ventral arms, as in *Ommatostrephes*; base of left ventral arm with scalelike processes. HOYLE, 1891.

Illex: One of the ventral arms as in *Ommatostrephes*; arms with large suckers. PFEFFER, 1900.

Histioteuthidae

Calliteuthis: Both dorsal arms; suckers at the tip small, biserial, situated on palisade-like pads. CHUN, 1906.

Histioteuthis: Both dorsal arms; suckers at the tip small, quadriserial, situated on palisade-like pads. CHUN, 1906, Plate XXI.

Cranchiidae

Cranchia: Right ventral arm; suckers mostly quadriserial, densely arranged on the dorsally curved tip. Arm thick with large keel. Third pair of arms with small, densely arranged suckers at the tip. CHUN, 1906, Plate L, Figure 1.

Liocranchia: Left ventral arm more strongly developed than right arm, with paired proximal and uniserial distal suckers. CHUN, 1906, Plate LI, Figure 9.

Euzygaena: Right ventral arm more strongly developed than left arm, with a large keel and densely arranged biserial suckers. CHUN, 1906, Plate LII, Figure 3.

18 Buccal funnel and attachments

The buccal funnel, which projects from the base of the pharynx, consists of a buccal membrane, the buccal pillars and their attachments.

I use the term buccal pillars for the radial supports directed toward the base of the arms, which consist mainly of longitudinal muscle fibers. The buccal pillars are usually spindle-shaped, with a tapering free apex and a narrowed base from which the fibers extend into the surrounding musculature. The **buccal membrane** is extended like a sail between the buccal pillars and forms points at their apexes.

The 8-radiate form of the buccal funnel of the Enoploteuthidae is probably the primitive condition. The buccal pillars are more or less radial and equally spaced (Plate II, Figure 6; Plate VIII, Figure 1). In the pterygiomorphous Enoploteuthidae, the two dorsal pillars are approximated and become altogether contiguous in the adults. This condition is transitional to the 7-radiate funnel of the other Oegopsida, in which the dorsal pillars are fused. The ventral pillars, too, are often approximated and, in old specimens of *Histioteuthis* and in the Veranyidae, fused. In the latter case, the buccal funnel becomes 6-radiate.

The smaller number of buccal pillars therefore does not indicate a primitive condition but is secondary, since the ventral pillars are separate in the young stages of those forms in the adults of which they were found fused.

The **pillars** are pervaded their whole length by nerves which, like the nerves of the arms, form a swelling and have a peripheral cover of ganglion cells (Plate III, Figure 16). I found such knoblike swellings at the base of the 3rd pillar of *Thaumatolampas* and *Abraliopsis* (Plate II, Figures 6, 7;
19 Plate VIII, Figure 1). The nerves of these buccal pillars form a loop in those knobs, accompanied by a thick vein and a smaller branch of an artery (Figure 7). This structure has not yet been described and its function is not known. Since it is not covered with sensory epithelium, it may be assumed that it serves as a sensory organ for pressure.

The often intensively pigmented **buccal membrane** may bear longitudinal folds or be smooth on

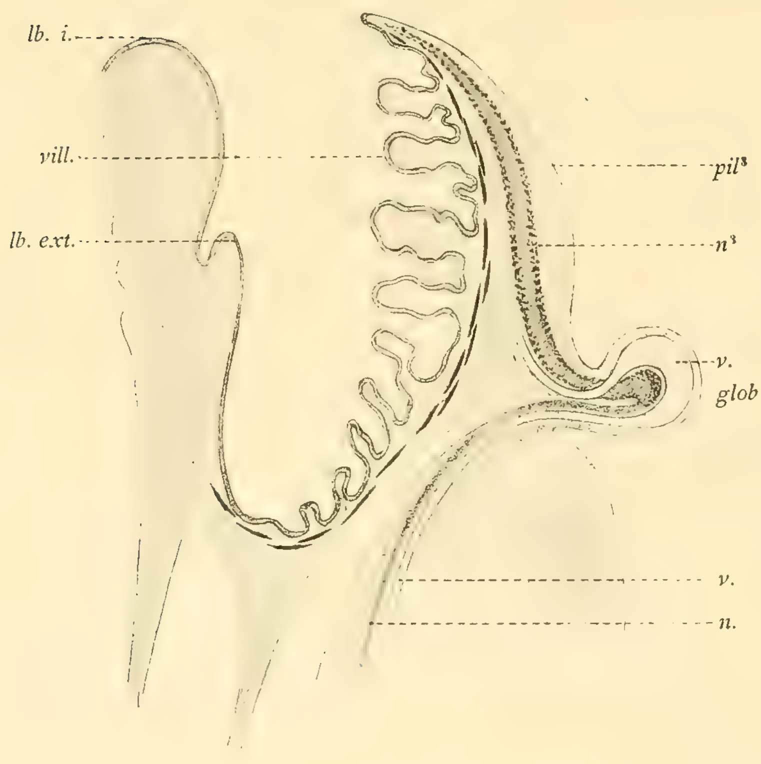

FIGURE 7. Longitudinal section of the buccal funnel of *Thaumatolampas* at the 3rd buccal pillar:

glob. knob of third pillar; *lb. i.* inner lip; *lb. ext.* outer lip; *n.* nerve; n^3 thick part of nerve of pillar, covered with ganglion cells; pil^3 3rd buccal pillar; *v.* vein; *vill.* villi of buccal funnel.

the outer surface; its inner surface forms transverse or longitudinal wrinkles and sometimes bears villi, covered with glandular epithelium (*Thaumatolampas*—Figure 7, *Abralia*, *Abraliopsis*). In rare cases (*Benthoteuthis*), the buccal tips bear small suckers (Plate XXV, Figure 3).

In *Pterygioteuthis* the buccal membrane, midway between its buccal pillars, is fused with the protective membranes which extend in sail-like form between the arms (Plate XIII, Figure 7).

The **attachments** of the buccal pillars represent muscle cords which extend to the base of the arms without actually passing into the protective membranes. The position of these attachments, although it shows characteristic systematic differences, has not been described by earlier observers; the following details are therefore given:

The attachments of all Oegopsida end dorsal to the suckers on the 1st and 2nd arms, and ventral to the suckers on the 3rd arms. The families can be grouped as follows, according to the position of the attachments of the 4th arms:

Ending of the attachments of the 4th arms

dorsal	*ventral*
Enoploteuthidae	Onychoteuthidae
Ommatostrephidae	Thysanoteuthidae
Histioteuthidae	Gonatidae
Bathyteuthidae	Veranyidae
	Tracheloteuthidae
	Chiroteuthidae
	Cranchiidae

It is not known whether this condition reflects a closer relationship between the above families. It is noteworthy, however, that the Tracheloteuthidae, Chiroteuthidae and Cranchiidae also show similarities in the structure of the funnel depressors.

I name the spaces between the buccal funnel and the bases of the arms "**buccal pockets**". Depending on the number of pillars, the space beween buccal funnel and the base of the arms is divided by delicate membranous septa into 8, 7 or 6 pockets; these septa extend downward from the points where the attachments to the buccal pillars originate and pass to the bases of the arms. The openings of the pockets so formed have been called "pori aquiferi" because of their resemblance to the opening of the pockets into which the Myopsida retract their tentacles or to the openings leading to the cavities filled with water in some Octopoda (*Tremoctopus*). I shall retain the term "pori aquiferi", even though those structures are completely different. The number of openings of the buccal pockets is never more than 6, because the dorsal and ventral pockets of the 8-radiate buccal funnel of the Enoploteuthidae are covered by a membrane. In the Ommatostrephidae and some other families there are only 4 "pori aquiferi" because the pockets between the 2nd and 3rd arms are also covered by membranes.

The septa between the buccal pockets are sometimes absent, most frequently between the 3 ventral pockets.

Deep attachments of the arms. I observed another two—more or less distinct—categories of attachments that connect the bases of the arms. There are conical muscles which orginate on the ventral surface of the base of the arms and taper toward the adjacent arm, i.e. from the 1st to the 2nd, and from the 2nd to the 3rd arm (Plate VIII, Figure 1). The muscles extending from the 3rd to the 4th arm are cordlike and pass below the attachments of the ventral arms, crossing each other so that they form a kind of chiasma (Plate X, Figure 1).

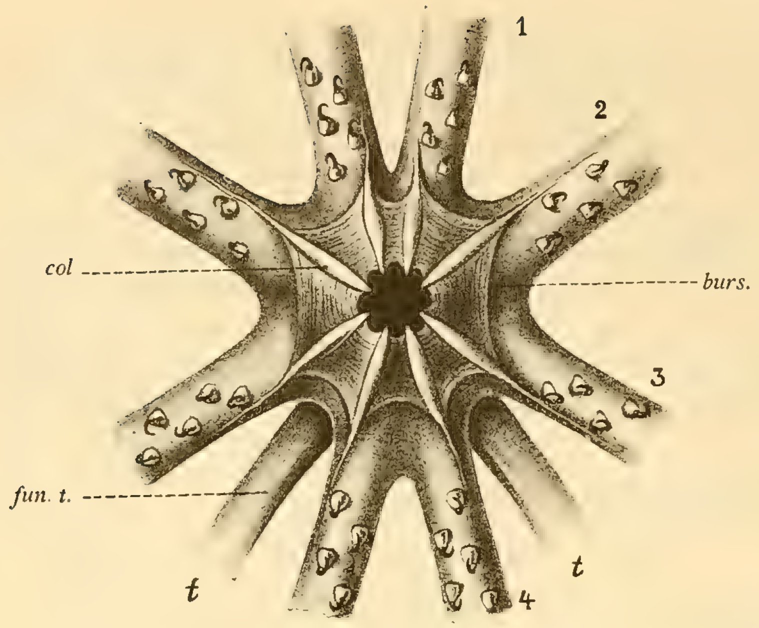

FIGURE 8. Diagram of the attachments in the Enoploteuthidae. Dorsal attachments of the 4th arms. Eight-radiate buccal funnel:

1, 2, 3, 4 1st to 4th arms; *t* tentacle; *burs.* opening (porus aquiferus) of a buccal pocket; *col.* buccal pillar; *fun. t.* thin muscle of attachment for the tentacle.

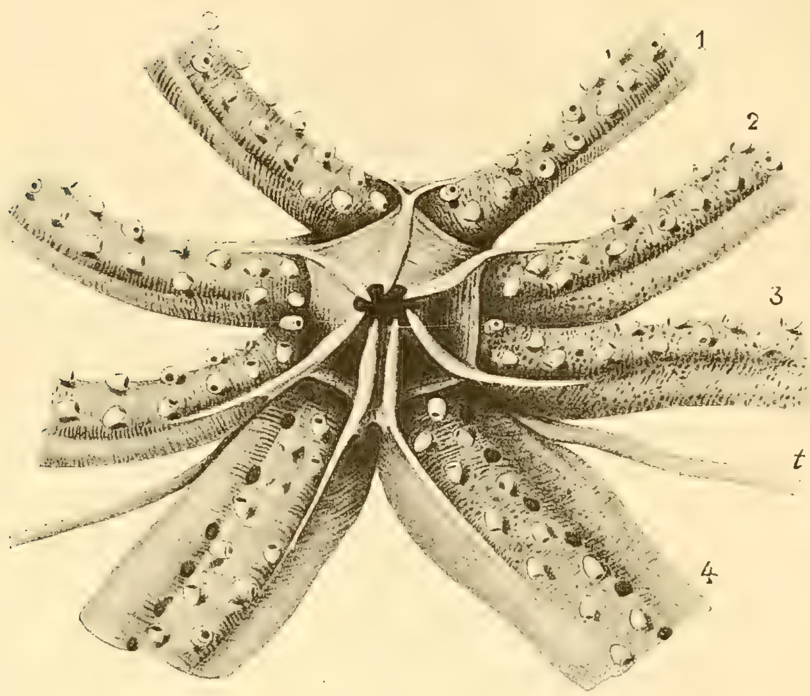

FIGURE 9. Attachments in *Chiroteuthis.* Ventral attachment of the 4th arms. Seven-radiate buccal funnel:

1, 2, 3, 4 1st to 4th arms; *t* tentacle.

21 The deeper attachments pass in the opposite direction: they extend from the dorsal surface of the bases of the arms to the ventral surface of the preceding pair of arms, i.e. from the 4th to the 3rd arms (Plate II, Figure 7), from the 3rd to the 2nd and from the 2nd to the 1st arms.

The function of these attachments has the following effect: the attachments extending from the buccal funnel draw the arms close together above the buccal funnel, which position is supported by the deeper, oblique attachments.

Gladius

The systematic importance of the gladius has been stressed by all early authors. Recently, Jatta, Hoyle and Pfeffer treated the subject particularly thoroughly. I therefore refer to the earlier descriptions, confining myself to a description of the gladius of some rarer forms, such as *Mastigoteuthis* and *Cranchia*.

The gladius consists of a rhachis which gradually tapers posteriorly and often bears sharply projecting ridges, usually a median and two lateral ridges. The gladius bears lateral chitinous lamellae, which may be wider or narrower or even quite reduced. These lamellae, together named "flag", are always present at the posterior end of the rhachis, where they are often confluent ventrally and their margins fuse to form a cone which may be spoon-shaped or oblong-conical. Seldom is any indication of a cone lacking. In respect to the formation of the gladius in the pocket-like shell gland, the reader is referred to the description of *Chiroteuthis*. Whether the chambering described for this genus (Plate XLI, Figure 13) is the last reminiscence of an ancient condition is as yet hard to decide.

Coloration

As in all Cephalopoda, the coloration of the Oegopsida is caused mainly by the chromatophores. Chromatophores are always present, even in those Cranchiidae which are almost completely transparent in life. According to Joubin (1892), the arrangement of the chromatophores is symmetrical in the young forms, but later the regular pattern is more or less obliterated by the formation of further chromatophores. Nevertheless, on the head, eyes, and base of the fins, symmetry in the arrangement of the main chromatophores is present throughout life.

The chromatophores are always embedded in the cutis, usually arranged in a superficial and a deep layer.

The structure and development of the chromatophores will be described in a separate chapter. Noteworthy within the present context is, however, that the chromatophores are not the only carriers of pigment. In purple or red forms the coloration is intensified by the presence of ramified connective tissue cells filled with a granular pigment (*Mastigoteuthis*, Plate XXXVII, Figures 1–3; *Benthoteuthis*, Plate XXVII, Figure 8; *Pterygioteuthis*, Plate XVI, Figure 5).

22 In general the coloration is restricted to the outer surface of the body but it may extend also to the mantle cavity. Thus, in the Histioteuthidae and especially in *Calliteuthis ocellata*, the gills and inner surface of the mantle are purple-red. *Abraliopsis* (Plate IX, Figure 2) has an intensively red penis, the wall of the visceral sac is reddish and the intestine is dark. Especially conspicuous is the purple stomach of the Histioteuthidae. Other organs intensely colored in life are the ink sac and the liver; the latter is usually brown, but in *Doratopsis* it is red.

In addition to this coloration which is caused by pigments, there is also a "structural coloration", caused by the effect of thin lamellae, which was described by Brücke (1852, p. 33). Structural coloration causes the metallic sheen of the iris and of the capsule of the ink sac; it appears also on various parts of the outer surface of the body, especially in the Enoploteuthidae. Sections show that the golden or silvery sheen is caused by interference from undulate lamellae of connective tissue.

INTERNAL ORGANIZATION

Nervous system

The work of Hancock (1852) on *Ommatostrephes* is the only exact description of the nervous system of Oegopsida. Later observers, such as Brock (1880), Appellöf (1889, 1890) and Posselt (1890) contributed only minor details. Since I find it desirable to present an exhaustive description of the central and peripheral nervous system, I sacrificed a large specimen of *Chiroteuthis imperator* for this purpose, despite its rarity.

The **central nervous system** of the Oegopsida comprises 4 major centers—a cerebral, visceral, pedal and brachial ganglion—and the superior and inferior buccal ganglia (Figure 10). The Oegopsida are characterized by a sharp separation of these centers of which the brachial ganglion is an anterior projection of the pedal ganglion. Particularly striking is the large distance between the buccal ganglia and the central brain mass. In *Chiroteuthis*, which has an unusually long, cylindrical head (Plates XLI, XLIII), this condition is extreme, compared to other Cephalopoda. I regard this differentiation of the ganglia as constituting a primitive condition from which the concentrated nervous system of the Myopsida, and especially of the Octopoda, developed. While Ihering (1877) considers precisely the concentration of the nervous system of the Octopoda to be a primary condition, I find it hardly possible that such highly developed Cephalopoda as the Octopoda, standing, as they do, at the evolutionary end of the cephalopod chain, should have retained a primitive condition, and of the nervous system at that.

24 The **peripheral nervous system** differs little from that of the Myopsida. As our knowledge of the structure of the nervous system of the two groups is still incomplete, it it difficult to determine whether the conditions in the Oegopsida are primitive or not. A few special characters are briefly described below.

The optic nerve is always very short in those forms in which the eyes are situated close together, e.g. in *Chiroteuthis*; the stalk-eyed Cranchiidae, on the other hand, have an extremely long optic nerve (Plate LV, Figure 3; Plate LVI, Figure 9). The superior ophthalmic nerve and the inferior ophthalmic nerve, the latter originating from the pedal ganglion (Figure 11), are also longer in stalked eyes.

In *Chiroteuthis*, the main stem of the pallial nerve shows the most primitive condition so far observed in the Cephalopoda: it is not divided into an inner and an outer branch and encloses the stellate ganglion completely (Plate XLI, Figure 3). In other Oegopsida, e.g. *Chaunoteuthis* (Appellöf), *Ommatostrephes* (Hancock, Brock) and *Gonatus* (Hoyle), however, such a branching does exist, and also involves displacement of the stellate ganglion.

According to previous descriptions, 5 brachial nerves originate on each side from the brachial ganglion. In *Chroteuthis* there are only 4 such nerves, because the nerve of the tentacles originates secondarily from the 4th nerve of the arms.

Eyes

The eyes are rarely spherical; usually they are elliptical or oval, due to the shortening of the main axis. If they are oval, their anterior end is narrower than their posterior end. The bilateral symmetry caused by the position of the optic ganglion on the posterior surface of the eyeball is reflected in the form thereof. This condition is most distinct in the pretty eyes of *Benthoteuthis*. Some deep-sea forms, on the other hand, show a lengthening of the main axis and a tendency to develop a telescopic

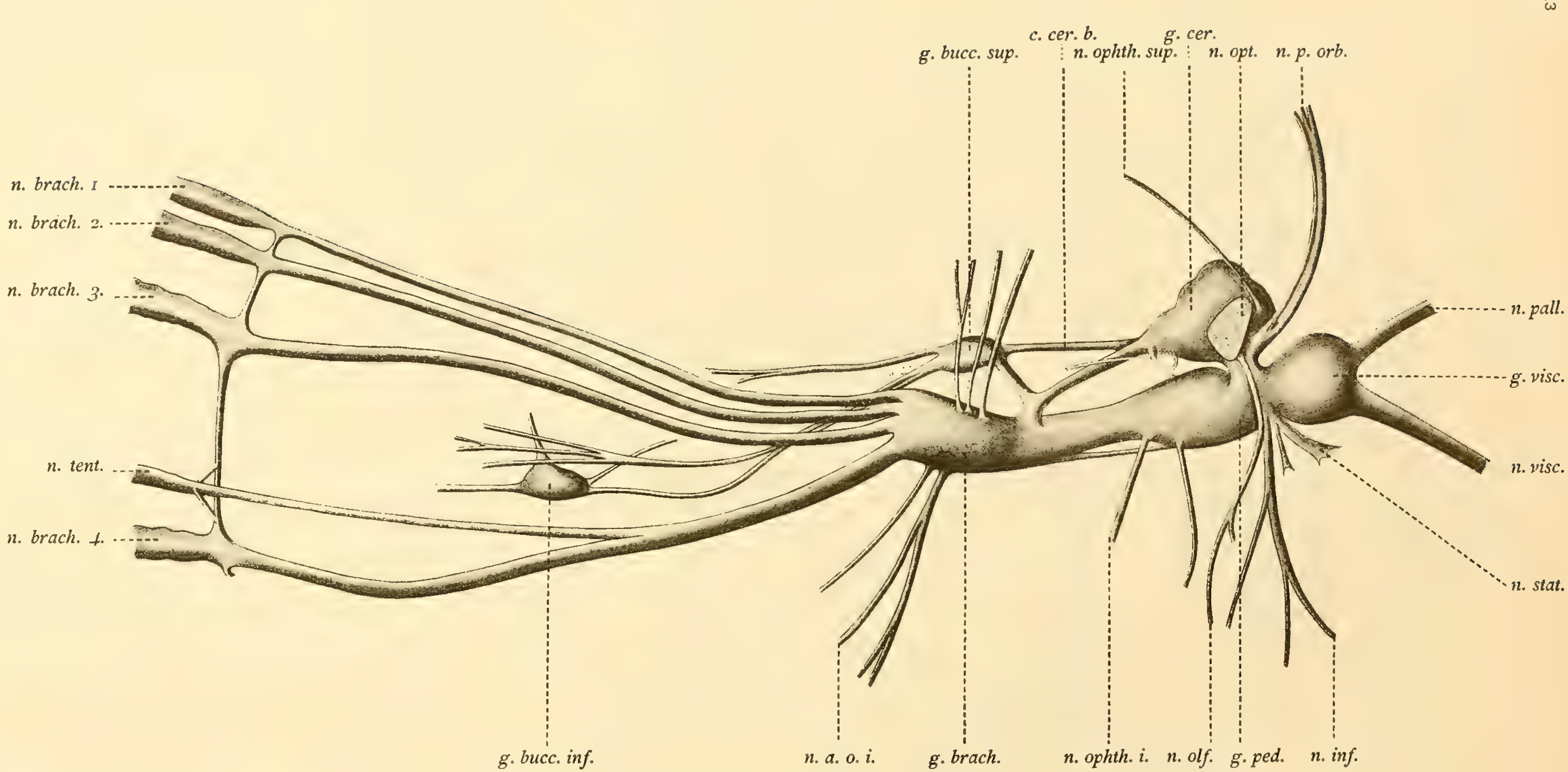

FIGURE 10. Nervous system of *Chiroteuthis imperator*, lateral view:

g. cer. cerebral ganglion; *g. brach.* brachial ganglion; *g. ped.* pedal ganglion; *g. visc.* visceral ganglion; *g. bucc. sup.* superior buccal ganglion; *g. bucc. inf.* inferior buccal ganglion; *c. cer. b.* cerebro-buccal commissure. Nerves originating from the cerebral ganglion: *n. opt.* optic nerve; *n. olf.* olfactory nerve; *n. ophth. sup.* superior ophthalmic nerve; *n. p. orb.* postorbital nerve. Nerves originating from the pedal ganglion: *n. inf.* funnel nerve; *n. stat.* nerve to the statocyst; *n. ophth. i.* inferior ophthalmic nerve. Nerves originating from the visceral ganglion: *n. pall.* pallial nerve; *n. visc.* visceral nerve. Nerves originating from the brachial ganglion: *n. brach. 1, 2, 3, 4* the 4 nerves to the arms; *n. tent.* nerve to the tentacle; *n. a. o. i.* inferior antorbital nerves (the superior antorbital nerves originate at the level of the superior buccal ganglion).

eye (*Calliteuthis*, Plate XX, Figure 1; *Benthoteuthis*, Plate XXVII; *Toxeuma*, Plate LVI, Figure 10).

Eyes which do not project markedly from the head are called sessile. Some forms have eyes which project half or completely from the head surface (*Desmoteuthis*, *Taonius*). "Stalked eyes" project from the head on a longer or shorter basal part. The stalks are either short and thick (*Teuthowenia*), as long as the eye, or several times longer than the eyeball (*Crystalloteuthis*, *Toxeuma*, *Euzygaena*, *Sandalops*, *Corynomma*, *Bathothauma*). The usually ovoid stalked eye often has its pointed anterior surface directed ventrally, while the broader posterior surface is directed dorsally. In addition, the connective tissue at the anterior margin is sometimes thickened into a point resulting in a sandal-shaped eye (*Sandalops*).

The size of the eyes relative to the entire body varies widely. The eyes are small in *Euzygaena*, medium-sized in most species, and very large in adult Histioteuthidae, Chiroteuthidae and in other giant specimens of Oegopsida occasionally observed. *Chiroteuthis* has probably the largest eyes relative to the size of its body (Plate XL).

Regarding a detailed anatomy of the eye of Oegopsida, the reader is referred to my earlier communications (1903) and to the chapter on *Benthoteuthis* (Plate XXVII).

Since in these descriptions we are mainly concerned with the eyes of deep-sea forms, there is one point that merits attention. All Oegopsida are pelagic organisms of which only few forms have adapted to life near the surface. The majority inhabit the dark depths and only exceptionally rise to the surface.

As there is little information on their normal depth range, it can be judged only indirectly whether adaptations to life in the dark depths have indeed taken place. The only source of information is, in my opinion, the condition of the retina. As demonstrated first by RAWITZ (1891) and later very thoroughly by HESS (1905), the pigment of the retina reacts to darkness or light with great exactitude. If Cephalopoda are kept in the dark, the pigment is retracted completely to the bases of the rods, leaving the rods free of pigment. If Cephalopoda are exposed to the light, the pigment concentrates at the apex of the rods, near the limiting membrane, forming a dense, uniformly black layer. It was therefore expected that in forms adapted to life in great depths, the pigment would assume the position characteristic for darkness. This is in fact the case: the layer of rods of deep-sea forms examined proved to be completely free of pigment (*Benthoteuthis*, Plate XXVII).

Another condition distinguishing the eyes of deep-sea fishes is that the rods are often extremely thin and long. HESS noted that in surface-inhabiting Cephalopoda, the length of the rods increases toward the margin of the retina, while there is a "stripe" of narrow, densely arranged rods in the cen-

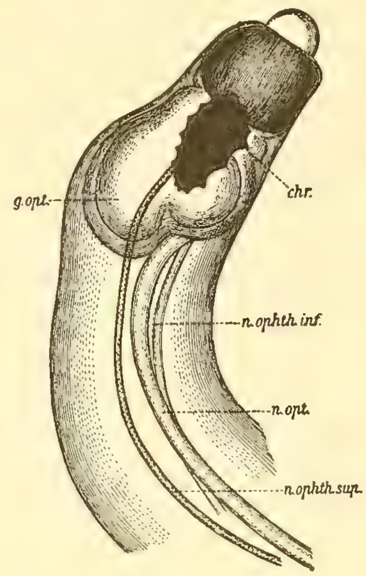

FIGURE 11. Stalked eye of *Corynomma speculator* CH., dorsal:

n.opt. optic nerve; *g.opt.* optic ganglion; *n.ophth.sup.* superior ophthalmic nerve; *n.ophth.inf.* inferior ophthalmic nerve; *chr.* chromatophore.

tral parts. On assuming this stripe to expand beyond the center of the retina while the rods become shorter and thicker toward the periphery, one obtains the picture characterizing the condition in deep-sea Cephalopoda. Furthermore, I found an area of optimal vision in at least one deep-sea form, *Benthoteuthis*, which already showed the characteristics of a fovea, in which the rods are longer and more densely arranged than in all other parts of the retina; indeed, they are the longest rods so far known in any animal whatsoever. This density of the rods also affects the form of the sensory cells.
26 In surface forms, these cells form a simple sensory epithelium in which the nuclei are situated in about the middle of the cell. In deep-sea forms, cells of this form are present only at the margin of the retina. Where the rods are densely arranged, the sensory cells form long, threadlike fibers and their nuclei are, due to the swellings they cause, displaced to different levels. Thus sections of the central part of the retina show 6–8 superimposed layers of nuclei—a condition not observed to such a degree in the stripe of the retina of surface Cephalopoda.

The eye is surrounded by a duplication of skin or **lid fold**; it leaves the anterior side of the eye free, so that water comes in direct contact with the lens, iris and a large part of the eyeball. Contraction of the radial muscle fibers of the lid fold causes partial or complete closure of the opening. In the latter case, part of the lid membrane may protrude like a hernia; this is sometimes observed in preserved specimens (*Liocranchia*, Plate LI, Figure 5).

In *Chiroteuthis*, the circular musculature is thickened at the posterior margin of the fold into a crescent-shaped pad. At the anterior margin the lid fold usually forms a more or less pronounced depression or "eye sinus". In many families however, this sinus is only weakly developed or altogether absent.

It was the structure of this lid fold that gave rise to the name "Oegopsida". In the higher developed Myopsida the lid fold covers the lens and becomes a transparent cornea with only a small opening. This character is generally considered to be of great systematic importance. However, it is not characteristic for all Myopsida, and its systematic importance has been greatly overestimated, as will be shown later in the description of *Spirula*.

Olfactory tubercles

The **olfactory tubercles** of the Oegopsida always form papillae and are never situated in pockets. In forms with 3 neck folds, the olfactory tubercles are thickenings of sensory epithelium on the median fold; if such folds are absent, the tubercles are situated in the same position in the form of rounded knobs or of nodules having short or longer stalks (*Desmoteuthis*, Plate LIV, Figure 6). The olfactory tubercles of *Chiroteuthis* and *Doratopsis* are a ringlike pad with a beak-shaped process and are situated on a long, transparent stalk (Plate XL, Figure 5). The epithelium consists of sensory cells, which have been described in detail by Watkinson (1908), and ciliated cells between the former. The olfactory nerve, which reaches the olfactory tubercle, is visible in transparent forms along the stalk and beneath the skin to the region of the orbit.

Intestinal tract

Whether the intestinal tract of the Oegopsida differs very much from that of the Myopsida has
27 not yet been sufficiently investigated. The two groups do, at any rate, differ markedly in the structure

of the large glands associated with the intestinal tract, which I name liver, salivary gland and pancreas.

The mouth, which bears two jaws, is surrounded by two circular **buccal lips.** The outer lips are always smaller, and the inner lips always show a characteristic folding. Only in old specimens of *Histioteuthis* did I find such a folding on the outer lip, too. The outer lip of the latter usually forms a narrow rim.

The **jaws** and **radula** differ little from those of the Myopsida. The radula varies widely in form, not only within the same family, but also within the same species.

The **pharynx**, described in detail by Heinrich (1904), shows a number of primitive characters in the arrangement of the musculature in *Ommatostrephes*.

The esophagus is directed obliquely ventrally and opens in the stomach to the accessory stomach (caecum, spiral stomach of Grant, pancreatic stomach of Owen) which is attached on the left side. The stomach and caecum extend anteriorly to the posterior side of the liver, except in the Cranchiidae, in which they end a marked distance from the liver. The short mid-intestine, which contains longitudinal folds, originates from the caecum. It forms a posterior loop in *Chiroteuthis* and passes more or less distinctly delimited into the rectum. The anus is bordered by a dorsal and a ventral lip between which the lateral anal appendages are always distinct. The abdominal wall projects into a kind of suspensory ligament near the anus. As stressed already by Prosch (1847), the whole intestinal tract forms a loop which extends from the dorsal to the ventral side, and stomach and caecum are suspended on the left and right side on the convex posterior part of the loop. This loop is very long in some Cranchiidae; in *Liocranchia* it shows a unique feature in that the esophagus, mid-intestine and pancreatic duct form numerous spiral coils (Plate XLI, Figure 13).

The relative size of the stomach and caecum depends to a large extent on the amount of food in them, but there are some constant differences. The caecum is usually smaller than the stomach (Enoploteuthidae, Veranyidae, Ommatostrephidae, Gonatidae); it is very small in *Teuthowenia*, *Desmoteuthis*, *Crystalloteuthis* and *Bathothauma* (Plate LVII, Figures 1, 6). The difference is less marked in *Benthoteuthis* and *Chiroteuthis*. In *Mastigoteuthis* (Plate XXXVI, Figures 1–4), stomach and caecum are of about the same size, while in *Brachioteuthis* (Plate XXXII, Figures 3, 4) and *Cranchia* the caecum is markedly larger than the stomach.

This proportion may change in favor of the caecum during post-embryonic development, as, for instance, in the larvae of *Chiroteuthis*, i.e. *Doratopsis* (Plate XLVII, Figure 5), compared with the adult *Chiroteuthis* (Plate XLII).

The **stomach** is usually sac-shaped, thick-walled and muscular, with longitudinal folds which are
28 covered with a thick cuticular layer; this layer, however, usually does not extend to the posterior part of the stomach. This part of the stomach is often thin-walled, without folds, and conically pointed, so that the whole stomach may be described as more or less distinctly divided into two parts. In some Cranchiidae, however, the stomach is distinctly divided into 3 parts: a long, tubular anterior part is followed by an onion-shaped middle part with large longitudinal folds, which passes into a large, thin-walled terminal part (Plate LIV, Figure 18). In *Bathothauma* (Plate LVII, Figure 1), the thin-walled end part of the stomach is folded ventrally and anteriorly.

Neither stomach nor caecum is colored; only in the Histioteuthidae is the stomach deep-purple or brownish-red.

The **caecum** receives ducts from the liver which are covered with pancreatic glands. It bears sickle-shaped folds which converge more or less spirally toward the opening of the hepato-pancreatic duct. These folds may be restricted to the anterior part of the caecum or cover the whole organ to the posterior end. The ducts open into the anterior part, which is often differentiated from the posterior

part as a hoodlike formation. The posterior part forms either a sac or ends in narrow processes.

The entrance from the caecum to the stomach bears a sickle-shaped projecting fold (Plate LII, Figure 6. *vel.*). A groove with thick, swollen margins extends from the confluence of the spiral folds to the beginning of the mid-intestine (Plate L, Figure 12) which, in *Bathothauma*, is unusually wide.

The whitish, flocky chyme in the stomach and caecum gives no information about the food consumed. Even when solid remains are still present in the stomach, the action of the jaws and radula makes recognition of the prey impossible. Only in the stomach of *Thaumatolampas* did I find fragments of shells and soft parts, which apparently were those of Pteropoda, and legs of small Crustacea. The spiral folds apparently assist the uniform distribution of the digestive juices and the passage of the liquefied food to the mid-intestine.

The **liver** is entire in all Oegopsida and never bilobed as in most Myopsida. Nor is it ever pervaded by the esophagus and aorta, as is the undivided liver of the Loliginidae. The liver is usually spindle-shaped or oval (*Brachioteuthis*, Plate XXXII, Figures 3, 4) and is covered with a layer of connective tissue which frequently has a metallic sheen (*Desmoteuthis*, Plate LIII, Figure 1). If such a sheen is absent, it appears brown or blood-red (*Doratopsis*).

Benthoteuthis (Plate XXVI, Figures 2, 3) has a liver of unusual form. It has the shape of a sac, with two small, rounded anterior projections. The hepatic parenchyma is present only in the posterior third and extends for some distance on the ventral side as a lining of the wall; the other part of the liver is thin-walled and filled with a clear liquid.

The liver usually forms an acute or right angle with the longitudinal axis of the body; in some cases (*Bathothauma*), it projects far into the mantle cavity. The liver of *Thaumatolampas, Chiroteuthis*
29 and *Benthoteuthis* is situated in the longitudinal axis.

The **bile ducts** originate ventrally near the posterior or dorsal end of the liver, surround the mid-intestine and open jointly in the hood of the caecum. In *Bathothauma* and *Benthoteuthis* (Plate XXVI, Figures 1, 2) they bend anteriorly in a convex curve. The Cranchiidae have an extremely long common duct, resulting from the fusion of the two bile ducts. The common duct accompanies the esophagus and mid-intestine for a considerable distance; in *Liocranchia* it forms spiral coils.

The **pancreatic appendages** vary strikingly in form. Sometimes they cover the whole bile ducts; in other cases they form a compact mass around the liver but leave the common duct free (*Cranchia*, Plate L, Figures 6–8; *Liocranchia*, Plate LI, Figure 13); sometimes they surround the caecum some distance from the liver (*Leachia*, Plate LII, Figure 5). In *Tracheloteuthis* and *Cranchia*, I found asymmetrical pancreatic appendages, more strongly developed on the left side. The pancreas may also form compact glandular lobes, which are few in *Chiroteuthis* (Plate XLII, Figures 2–4) and more numerous in *Brachioteuthis*. In *Thaumatolampas*, *Desmoteuthis* and *Crystalloteuthis* the pancreatic ducts decrease in size and are markedly well developed and numerous on the bile ducts (Plate LIV, Figures 12, 18).

Leachia and *Benthoteuthis* (Plate XXVI, Figures 1, 2) have thin-walled, vesicular, grape- or mulberry-shaped pancreatic appendages; in *Leachia* they form several broad ducts which open in the widened end part of the hepatic duct.

The **salivary glands** of the Oegopsida form anterior and posterior pairs, and their ducts open into the pharynx.

The **posterior salivary glands** are situated outside the head (cranium), pressed against its posterior surface (*Chiroteuthis*, Plate XLIII, Figure 3), and consist of two fused lobes with a shallow dorsal median groove for the esophagus, aorta and the two pallial nerves. The single salivary duct originates from the serrate anterior margin of the glands, accompanies the esophagus through the brain, passes ventral to the

subpharyngeal ganglia, is embedded in the ventral mass of the pharynx and opens anteriorly on the subradular organ.

Single posterior salivary glands are present in all Oegopsida; their paired origin is evident only in the paired beginning of their collecting ducts. They are also present in the Cranchiidae (Plate LVII, Figure 6), but OWEN (1836, p. 533) overlooked them.

The **anterior salivary glands** are paired and are situated at the border betweeen pharynx and esophagus, near the inferior buccal ganglia (*Chiroteuthis*, Plate XLI, Figure 2). According to unpublished studies of WÜLKER, they are divided in all Oegopsida (as in the Loliginidae) into an outer extrabulbar part and an inner intrabulbar part, connected by a duct. There are efferent ducts on each side, which remain separate and open anteriorly in the tongue pocket.

The **ink sac** is usually small; it is situated on the dorsal side of the rectum. It may be tubular or form a wide, saclike posterior part; the luminous organs of *Chiroteuthis* and *Corynomma* are situated on it.

Vascular system

The circulation of the Oegopsida requires a more detailed study. Though BROCK (1880), VIGELIUS (1880), APPELLÖF (1890) and POSSELT (1890) described the distribution of the vessels in some species, they failed to clarify some important points. My own studies should increase our knowledge, but fail to provide a comprehensive description of the circulation consistently applicable to the same species. I will therefore give a brief summary of my findings.

The **heart** changes strikingly in form depending on the state of contraction. It is situated on the ventral side of the posterior half of the liver, and may be cylindrical, spindle-shaped or oval. It sometimes protrudes toward the auricles, assuming the form of a bagpipe (*Desmoteuthis*, Plate LIV, Figure 14), as described already by MILNE EDWARDS (1858). According to BROCK (1880, p. 63), the heart is elongated in the direction of the two major vessels—the cephalic aorta and the posterior aorta. This is not always the case: in *Bathothauma* its transverse width, which is characterized by the entrance of the auricles, is equal to its length; in slender forms it is situated in the longitudinal axis of the body (*Brachioteuthis*, Plate XXXII, Figure 3), and in other cases (*Benthoteuthis*, *Bathothauma*) it lies almost transverse.

Arterial circulation. Only two major arteries originate directly from the heart: the cephalic aorta (anterior artery) and the posterior artery. The cephalic aorta passes to the right of the esophagus and on the dorsal surface of the liver. In the Cranchiidae, in which the liver is usually situated transversely and projects toward the mantle cavity, the cephalic aorta touches only the dorsal apex of the liver (Plate LIV, Figure 12). The cephalic aorta is slightly spindle-shaped and widened at the base and from it originates the gastric artery, the branches of which supply the stomach and caecum (*Leachia*, Plate LII, Figure 5). According to VIGELIUS (1880, p. 56) and APPELLÖF (1890, p. 16), the genital artery originates from the gastric artery in *Thysanoteuthis* and directly from the cephalic aorta in *Chaunoteuthis*, but BROCK (1880, p. 64) and POSSELT (1890, p. 318) consider the genital artery as a branch of the posterior artery. Since my specimens were immature and had no distinct genital artery, I can only state that in *Chiroteuthis* I considered a small branch of the posterior artery as the genital artery. At any rate, it is certain that the genital artery of the Oegopsida does not originate separately from the heart, as it does in the Myopsida.

After sending arteries to the liver and pancreas, the cephalic aorta bifurcates at the entrance to the cranial capsule and branches—as will be described more comprehensively for *Chiroteuthis* (Plate

31 XLI, Figure 5)—to the salivary gland, to the posterior surface of the cranium and, most important, to the always prominent ophthalmic artery which accompanies the superior ophthalmic nerve. The branches which pass along the esophagus and enter the brain form the pharyngeal and the brachial artery. The brachial artery passes on the ventral surface of the pedal and brachial ganglia; it then divides at the level of the inferior buccal ganglion into two main branches which supply the ventral arms, the tentacles, and the 3rd, 2nd and 1st arms with thick vessels.

The posterior artery is rarely swollen at the base. It sends off first a vessel directed anteriorly which I consider as homologous to the anterior artery of the Myopsida. This vessel supplies the branchial hearts, the heart muscle (POSSELT), the ventral wall of the renal sac, the ink sac, the rectum and the ventral luminous organs (*Chiroteuthis*). According to BROCK and POSSELT, the posterior artery also sends off the genital artery. It also sends off a thick branch, the pallial artery, which passes along the anterior margin of the median septum. Then it divides into two thick branches to the posterior end of the body, mainly to the fins (A. pinnales).

Venous circulation. The arrangement of the veins in the arm region to the exit of the vena cava from the brain has never been described in detail. In *Chiroteuthis* (Plate XLI, Figure 5), the large vena cava forms a caecum (*coec. v. c.*) which is visible through the ventral wall of the head in preserved specimens; it then turns ventrally and receives two veins from the sides of the skull which extend above the statocysts, as well as the single salivary vein. Closely behind the dorsal funnel organ, the vena cava passes to the thin abdominal wall, where it is clearly visible in all species and extends in a more or less sinuous fashion, depending on the state of contraction. The vena cava always bypasses the liver in a wide right-side curve and receives venous branches from the ink sac, rectum, liver and pancreas; it then divides into two branchial arteries which open into the branchial hearts. Before opening in the pulsating centers which contain valves, the branchial arteries receive on each side the pallial and abdominal veins.

At the end of the main stem of the vena cava and along both branchial arteries, along the hepatic and abdominal veins, there are venous appendages; these project into the renal sacs the thick epithelium of which covers them. These venous appendages are usually fused into a compact mass which extends to the branchial hearts and cannot be divided into separate parts. Only in the Cranchiidae do I find an almost constant and distinct differentiation of these "venous sacs", the striking variation of which will be described later (see Plate L, Figures 6, 7, 14; Plate LIV, Figures 12, 15; Plate LVII, Figures 2, 7).

The hepatic veins usually bear appendages their whole length and form an anterior (ventral) and a posterior (dorsal) sac. A sac of the gastric vein is also clearly differentiated from those situated at the end of the branchial arteries, before the branchial hearts and which receive the pallial and abdominal veins. Only in *Cranchia* could I find such sacs bordering on the branchial heart.

32 Particularly characteristic for the Cranchiidae is the great length of the branchial arteries, which are free of venous appendages in their greater part.

Of the other veins which so far were never described in the Oegopsida, the cephalic vein is noteworthy; it is sickle-shaped in cross section inasmuch as it surrounds the esophagus; in the Cranchiidae it forms a loop, swollen like an ampulla on the dorsal (posterior) apex of the liver (Plate L, Figure 7, *amp. v.*; Plate LIV, Figures 12, 18). At this point it receives the dorsal vein, later the pancreatic vein, and finally opens in the sac of the posterior hepatic vein (Plate LIV, Figure 15).

Two other vessels that were never described are the cardiac veins (venae cordis) which transport venous blood from the heart muscle to the branchial arteries (*Desmoteuthis*, Plate LIV, Figure 14).

The branchial arteries, which contain valves at their base, originate from the branchial hearts; on

the latter I found lateral and slightly dorsal appendages in all species, including species in which their presence had so far not been realized. The arterial blood is transported from the gills back to the heart by the branchial veins which are rarely widened into atria; at their entrance to the heart there are once more valves.

Comparing the circulation of the Oegopsida as briefly described above with that of the Myopsida, one becomes aware of the wide gaps in our knowledge. Neither on the venous circulation of the anterior part of the body or the thickenings of the venous stems in the head, nor on the origin of some important arteries are we as yet sufficiently informed. The only assertion that can at present be made is that the genital artery does apparently not originate separately from the heart.

Gills

Whether the construction of the **gills** of the Myopsida bears any evidence of primitive conditions is as yet hard to say. Schäfer (1904) considers their gills to be more primitive than those of the Oegopsida, but since this opinion is based merely on his finds examining the gills of *Illex*, which contain a smaller number of radial and transverse folds than do the Myopsida, it is not convincing.

The gills of the Oegopsida are in general slender and—since their outer lamellae are larger than the inner ones with which they alternate—they are asymmetrical. The branchial vein (efferent vein) therefore passes not in the middle of the gill but slightly inward; the same is the case for the branchial nerves. The respiratory membrane bears a smaller number of radial and transverse folds than that of the Myopsida, but its surface is enlarged by secondary transverse and longitudinal folds.

The gill is attached to the mantle by a ligament. The branchial gland, which is embedded in this ligament, contains venous blood; its function remains obscure.

33

Excretory system

The renal sacs of all Oegopsida are fused in the middle and no partition indicates an original separation. However, the symmetrical position of their openings suggests that two separate sacs were originally present. The large, uniform renal sac is situated at the posterior ventral surface of the liver, enveloping it for some distance anteriorly and extending laterally to the branchial hearts. A dorsal evagination like that in the Myopsida has not been found in the Oegopsida (Vigelius, 1880, p. 31, *Ommatostrephes*).

Its dorsal wall borders on the heart, the venous sacs and the large branchial vessels; its ventral side reaches the thin abdominal wall. In preserved specimens, it is usually filled with a whitish clot which has to be removed to show the openings more clearly.

The outer openings of the renal sac are situated symmetrically, usually in the middle between the branchial hearts and the liver; they appear as slits with oval lips. It has been maintained that these openings are never drawn out in the form of a chimney, as is characteristic for the Myopsida; but this does definitely not apply to all the Oegopsida. Lönnberg (1896) stressed that the renal openings of *Thysanoteuthis*, *Histioteuthis* and *Chiroteuthis* have the form of a chimney. I found similar formations also in the Cranchiidae (*Cranchia*, *Bathothauma*).

The inner openings of the renal sac form trumpet-shaped ciliated coelomic canals situated on the ventral wall of the body cavity.

Body cavity

It is mainly due to the excellent studies of Hancock (1864), Vigelius (1880) and Grobben (1884) that we are well informed on the relations of the body cavity (secondary body cavity of Claus, Hatschek and Grobben) to the exit ducts of the genital products and to the organs of excretion. These studies have shown that the Oegopsida have remained more primitive in the sense that the body cavity is large and not reduced to narrow ducts, as is particularly the case in the Octopoda. All the viscera of the Oegopsida are freely suspended in the body cavity and connected with the body wall only by narrow mesenteries or ligaments. We do not know to what extent the body cavity, which is lined with an epithelium and partly ciliated, extends into the cephalic region. The body cavity is divided in the middle into 2 large sacs by a broad median mesentery which extends from the vena cava to the esophagus and to the dorsal surface. This mesentery is inserted on the dorsal side of the liver, but does not project beyond it, into the posterior part of the body where the gastro-genital ligament attaches the intestine and genitalia to the dorsal body wall.

34 The Cranchiidae, especially the genus *Cranchia*, have an unusually large body cavity. The mesenteric ligament, too, has a characteristic form: it is divided at its connection with the liver into two lamellae which form a rooflike structure on the dorsal surface of the liver and gradually widen toward the dorsal side of the body. The dorsal artery and vein extend over their ridges to the gladius (Plate L, Figure 7).

Grobben considers the "peritoneal pocket" as a separate part of the body cavity which surrounds the male genital ducts. As will be shown in the description of the genital ducts, this space is not a separated part of the general body cavity.

Genitalia

The **testes and ovaries** of young specimens are situated on the posterior dorsal side of the stomach and project freely into the body cavity. A ligament from this end of the stomach extends obliquely posteriorly and is attached to the dorsal side of the body. I use the term "gastro-genital ligament" for this strand of connective tissue which contains blood vessels and sometimes also longitudinal muscles. In *Mastigoteuthis* the earliest "anlage" of the genital glands is situated on this ligament and this is partly the case in *Chiroteuthis*, where however the genital gland gradually comes to surround it ventrally as it grows, forming two lobes which gradually expand to the dorsal side of the stomach, surround it and almost become contiguous ventrally (Plate XLI, Figure 20; Plate XLIII, Figure 1).

Except in *Calliteuthis* (Plate XX, Figure 7), the **male genital ducts** are always single and situated on the left side. *Calliteuthis* has paired genital ducts and also double hectocotyli; since the latter are formed by both dorsal arms, like those of *Histioteuthis*, this condition may perhaps be regarded as primary, from which the asymmetry of the other Oegopsida developed secondarily.

Since a more detailed description of the structure of the male genital ducts will be presented in another section, it is at this point emphasized only that the Oegopsida differ from the Myopsida in their differentiation of the seminal vesicle into three distinct parts, in the large size of the first part thereof and, especially, in the unusual length of the caecum at which the vas efferens begins.

As mentioned in the description of the body cavity, the male genital ducts are situated in a **genital pocket,** which Brock (1879, p. 16) described in detail as a completely closed "peritioneal pocket". Grobben (1884, pp. 14 and 15) generally confirms Brock's data but adds that the pocket is completely

closed, to judge from inflation of the pocket by air, and that it is connected with the male genital ducts only by a canal—as discovered by Brock in *Sepia.*

I found such a canal, which is equipped with cilia, in all mature Oegopsida (1905, p. 646). It opens between the 3rd part of the seminal vesicle and the prostate into the male genital ducts; it is long,
35 rather narrow, and only slightly widened at the end (Plate X, Figure 3; Plate XV, Figure 9), which opens into the peritoneal pocket by a so far unknown ciliated funnel (Plate XV, Figure 10). As Marchand (1907, p. 25) demonstrated in the live animal, the ciliated epithelium moves in the direction toward the genital pocket. *Calliteuthis* has two ciliated canals, corresponding to the paired male genital ducts (Plate XX, Figure 7).

The genital pocket is lined with simple epithelium. Grobben considers this as evidence that the pocket is a part of the secondary body cavity that is completely isolated from the capsule of the testis. He notes, however, that the significance of this pocket will have to be decided by embryological and comparative anatomical studies.

In an earlier communication I wrote of the Oegopsida (1905, p. 649) that their spermatophore pocket, the caecum of their prostate and sometimes also the end part of their seminal vesicle—which forms a caecum in young specimens—project freely from a pocket into the mantle cavity. This is particularly the case in *Illex illecebrosus*, the male genital ducts of which are shown in Figure 12. In this relatively large specimen, measuring 10 cm mantle length, the semicircular outline of a pocket situated below the base of the gills is visible between the branchial heart and appendage and the adjacent mantle veins. The above parts of the genital ducts project only little from this pocket. In mature specimens, which are only slightly larger than the male in Figure 12, the spermatophore pocket, the caecum of the prostate and the terminal part of the seminal vesicle project far anteriorly below the branchial veins and arteries into the mantle cavity. The caecum of the prostate is very long and resembles a penis, but it is shorter than the end part of the spermatophore sac; in the immature stage shown in the figure, however, the caecum of the prostate is longer than the end part of the spermatophore sac. A fine probe can be introduced deeply into the male gonoducts from the opening of the pocket. I thought at first that this "genital pocket", which opens to the outside, is completely separated from that part of the body cavity which, according to the descriptions of Brock and Grobben, surrounds the genital ducts. To
36 clarify these relationships, sections were made of the entire genital system. Surprisingly, I found that the genital pocket, which opens to the outside, extends far posteriorly and is identical with the cavity which Grobben named the "secondary body cavity". It thus became clear that the "peritoneal pocket" is not genetically related to the body cavity of the Cephalopoda but represents a caecum lined with ectoderm which opens to the outside. In the Myopsida and Octopoda, in which the development of this pocket has not been studied, the margins of this pocket adhere so closely to the terminal part of the spermatophore sac that they have become fused and form a completely closed space. In *Illex*, on the other hand, Marchand found that the genital pocket remains open even in the mature male.

Posselt is the only observer who noted the condition described above, but he did not realize its significance. This author (Posselt, 1891, p. 352) noted briefly that *Illex* has a sac in which the prostate and seminal vesicle are situated and which is perforated toward the mantle cavity by a slit through which the upper end of the caecum of the prostate projects.

37 To understand the morphological significance of the ciliated canal, it is of importance that the ciliated funnel opens not into the body cavity but to the outside, i.e. into a genital pocket formed by an invagination of the outer surface. (Figures 13 and 14 show the extent of this pocket and the manner in which the ducts are suspended in it). The first cross section passes at the level of the end of the ciliated funnel (*inf.*). There, the genital pocket (*sacc. gen.*) surrounds the third part of the seminal vesicle almost

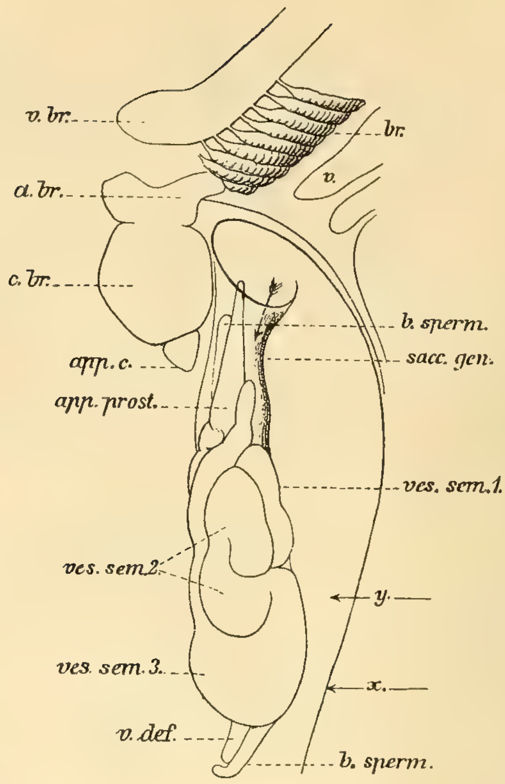

FIGURE 12. *Illex illecebrosus.* Genital ducts of an immature male. The arrow marks the entrance to the genital pocket:

c. br. branchial heart; *app. c.* appendage of branchial heart; *a. br.* branchial artery; *v.* branches of pallial vein; *v. br.* branchial vein; *br.* gills; *sacc. gen.* genital pocket; *v. def.* vas deferens; *ves. sem. 1, 2, 3* 1st, 2nd, and 3rd part of seminal vesicle; *app. prost.* caecum of prostate; *b. sperm.* spermatophore sac (Needham's sac); *x* level of cross section in Figure 13; *y* level of cross section in Figure 14.

completely, and the drawn-out swelling of the seminal vesicle is shown to be quite extensive. Only a narrow bridge of connective tissue connects the swelling with the other parts of the genital ducts; the latter are connected with each other by loose connective tissue. The greater part of the prostate projects freely into the genital pocket. The opening of the ciliated funnel, with its distinct cilia, is situated near the connective tissue which connects the prostate with the other part of the apparatus. In *Illex*, the funnel opening is broadly flattened and the cylindrical epithelium merges gradually with the flattened epithelium of the genital pocket. There is a caecum (*sac.'*), separated from the genital pocket, which is situated between the vas efferens and the spermatophore sac; this caecum was already described by Grobben, and we only add that it opens into the genital pocket only at the upper third of the genital ducts, which proves that it is a diverticulum of the genital pocket.

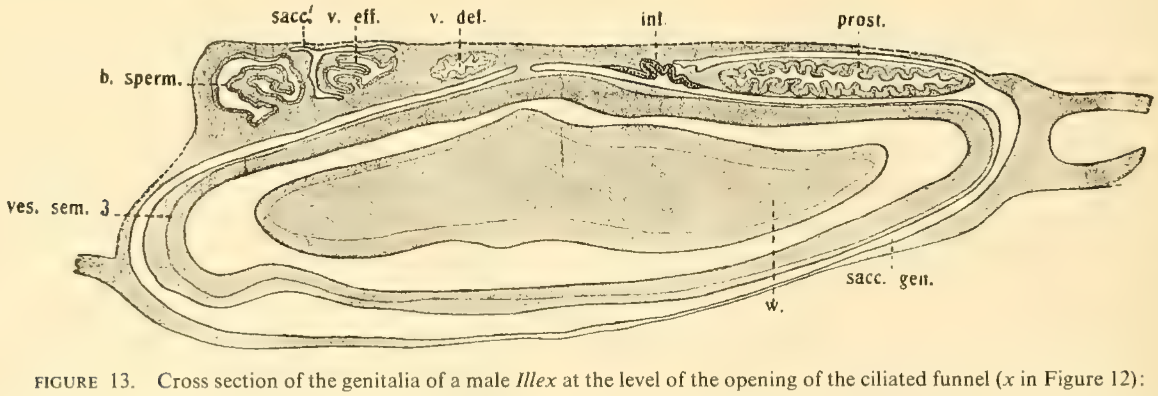

FIGURE 13. Cross section of the genitalia of a male *Illex* at the level of the opening of the ciliated funnel (*x* in Figure 12):

ves. sem. 3 3rd part of seminal vesicle; *w.* swelling of vesicle; *b. sperm.* spermatophore sac; *v. eff.* vas efferens; *v. def.* vas deferens; *prost.* prostate; *inf.* ciliated funnel; *sacc. gen.* genital pocket.

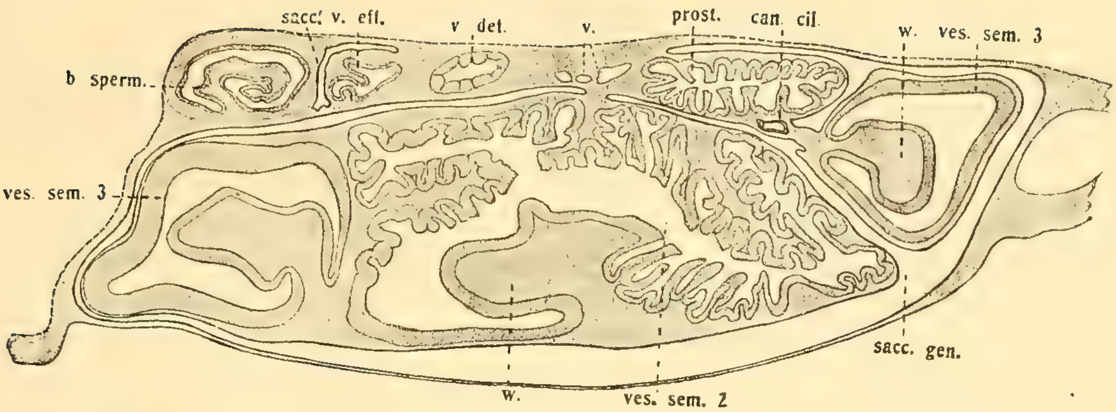

FIGURE 14. Cross section of the genitalia of a male *Illex* (at the level of *y* in Figure 12).

The descending branch of the 3rd part of the seminal vesicle is cut at the left, the ascending branch at the right. The swelling (*w.*) is recognizable in the second part of the seminal vesicle (*ves. sem. 2*), as in the 3rd part. *can. cil.* ciliated canal; *v.* blood vessels; *sacc.'* diverticulum of genital pockets between vas efferens and spermatophore sac. Other lettering as in Figure 13. A dashed line indicates the epithelium of the body cavity in Figures 13 and 14.

Figure 14 is a cross section at a slightly higher level; it shows that the large second part of the seminal vesicle and the adjacent proximal part of the first part of the vesicle project separately into the genital pocket and that the narrow bridge mentioned above is the only connection between them and the other parts. The distal part of the seminal vesicle also projects freely into the pocket. The ciliated canal appears in the cross section between the prostate and the seminal vesicle. Other details are explained in the legends; the dashed line represents the epithelium of the body cavity into which the vas efferens opens.

The **female genital ducts**—unlike those of the male—are nearly always paired. *Pterygioteuthis* is the only exception I know: it has a well-developed right oviduct, but no oviduct on the left side.

Since most of my specimens were immature or juvenile, all I can state is that the female genital ducts, like those of the male, always develop dorsal to the base of the gills. Their paired structure reflects a primitive condition, in contrast to the unpaired "anlage" of the left oviduct in the Myopsida. This view is confirmed by the work of Döring (1908), who demonstrated that the oviduct gland of the Myopsida is paired in the "anlage" but disappears secondarily on the right side. The oviduct gland is separated out from the ectoderm of the gill base pocket, while the oviduct develops from the coelomic epithelium. Not enough is known on the oviducts of mature females to venture a comparison with the Myopsida. All that can be said is that the oviduct glands swell considerably before oviposition and form a broad, gaping ring around the opening.

38 There are only two **nidamental glands.** Accessory nidamental glands, which are generally present in the Myopsida, are never present in the Oegopsida. The structure described by Weiss (1889) as accessory glands in *Chiroteuthis* later proved to be luminous organs situated on the ink sac; they will be described later.

The nidamental glands develop as ectodermal thickenings of the ventral visceral sac (Döring, p. 171); they later close up, groovelike (*Cranchia*, Plate L, Figure 6; *Benthoteuthis*, Plate XXVI, Figures 4, 5).

In striking contrast to the other Oegopsida, the genera *Abralia* and *Abraliopsis* have no nidamental glands, but possess instead greatly inflated oviduct glands.

Luminous organs

The **luminous organs** of the deep-sea Oegopsida deserve a more detailed description because of their peculiar formation and considerable variety of form. I described them in an earlier publication (1903); the following description is the result of more extensive studies.

The phosphorescence of the Cephalopoda was discovered by Vérany (*Céphalop. Médit.*, 1851, p. 116) in September 1834 near Nice. He enthusiastically described the magnificent coloration of *Histioteuthis bonelliana*, stressing that the peculiar blue spots on the ventral side of the mantle and arms are phosphorescent at night. He found similar luminous spots also in *Histioteuthis rüppellii* (p. 119). Since then, live specimens of this species have occasionally been caught by Nice fishers engaged in deep-sea fishing, but they were apparently never examined by zoologists, since none of the later publications mentions any phosphorescence. During the voyage of the *Valdivia*, however, we observed a slight phosphorescence in a specimen of the new genus *Thaumatolampas*. Factual information is thus limited to these few observations; but only exaggerated skepsis would reject the possibility that phosphorescence occurs in similar organs of other families of Cephalopoda, too.

On the finer structure of the luminous organs more is known than on their physiological significance. Much of our present knowledge we owe to Joubin and Hoyle, who published from 1893 onward a series of valuable descriptions on the luminous organs of Cephalopoda. They begin by describing the organs of *Histioteuthis*, *Chiroteuthopsis* and *Abralia* (Joubin, 1893, 1894, 1895). Hoyle then provided a new description on the luminous organs of *Pyroteuthis margaritifera* (1902), of *Pterygioteuthis* and *Abraliopsis* (1904) and of *Ancistrocheirus* (1905). Joubin (1905), finally published a detailed description of the eye organs of *Leachia cyclura*.

As to the **occurrence of luminous organs** in the Cephalopoda, it may be stressed that none are known in the Octopoda. Among the Myopsida, *Heteroteuthis* and *Sepiola* have luminous organs, as shown by Lo Bianco and by my pupils Th. Meyer and Marchand. These organs form two paired
39 glands, situated on the ink sac, which secrete a luminous substance (Th. Meyer, 1906, 1908). Similar glands in *Euprymna* and *Inioteuthis* are described in a still unpublished work by G. Wülker.

Although Hoyle (1907) recently published a list of Oegopsida that have luminous organs, a new list, which includes the most recent records, is in order and is given below.

Presence of Luminous Organs in the Oegopsida

Thaumatolampadidae		
Thaumatolampas diadema	Chun, 1902, 1903	Mantle cavity, eyes, tentacles
Enoploteuthidae		
Enoploteuthis leptura	Férussac and d'Orbigny; 1835–48, Chun	Mantle, funnel, head, arms, eyes
Thelidioteuthis alessandrinii	Troschel, 1857; Pfeffer, 1884, 1900; Verrill, 1883, 1884; Appellöf, 1889	Mantle, head, tentacle stalk
Ancistrocheirus lesuerii	Hoyle, 1905	Mantle
Abralia armata	d'Orbigny, 1835–48; Vérany, 1851; Joubin, 1895	Mantle, funnel, head, arms, eyes

Presence of Luminous Organs in the Oegopsida (contd.)

Enoploteuthidae (contd.)		
Abraliopsis morisi	Vérany, 1837; Joubin, 1896; Chun, 1902; Hoyle, 1904	Mantle, funnel, head, arms, eyes
Pterygioteuthis giardi	Chun, 1903; Hoyle, 1904	Mantle cavity, eyes
Pterygioteuthis gemmata	Chun, 1908	Mantle cavity, eyes
Pyroteuthis margaritifera	Rüppell, 1844; Vérany, 1851; Hoyle, 1902	Mantle cavity, eyes
Veranyidae		
Octopodoteuthis sicula	Chun	Ink sac (2 organs?)
Onychoteuthidae		
Onychoteuthis banksi	Hoyle, 1907	Mantle cavity
Chaunoteuthis mollis	Chun	Mantle
Histioteuthidae		
Calliteuthis ocellata	Owen, 1881	Mantle, head, arms
Calliteuthis reversa	Verrill, 1881; Chun, 1903	Mantle, head, arms
Calliteuthis hoylei	Goodrich, 1896	Mantle, head, arms
Calliteuthis meleagrina	Pfeffer, 1900	Mantle, head, arms
Histioteuthis rüppelli	Vérany, 1834; Joubin, 1893	Mantle, head, arms
Histioteuthis bonelliana	Vérany, 1834	Mantle, head, arms
Bathyteuthidae		
Benthoteuthis megalops	Chun, 1903	Arms
40 **Chiroteuthidae**		
Mastigoteuthis agassizii	Verrill, 1881	Mantle, fins, head, arms
Mastigoteuthis grimaldii	Joubin, 1893, 1895	Fins
Mastigoteuthis talismani	Fischer and Joubin, 1907	Fins
Mastigoteuthis cordiformis?	Chun, 1903	Mantle, fins, head, funnel, arms
Mastigoteuthis flammea	Chun, 1903	Arms, mantle, fins, funnel, head
Mastigoteuthis glaukopis	Chun	Eye corner
Chiroteuthis véranyi	Vérany, 1834; Chun, 1903	Mantle cavity, eyes, ventral arms
Chiroteuthis picteti	Chun	Mantle cavity, eyes, ventral arms
Chiroteuthis imperator	Chun, 1903	Mantle cavity, eyes, ventral arms
Cranchiidae		
Cranchia scabra	Pfeffer, 1900; Chun, 1908	Eyes
Liocranchia valdiviae	Chun, 1908	Eyes

Presence of Luminous Organs in the Oegopsida (contd.)

Cranchiidae (contd.)

Leachia cyclura	Grant, 1833; Joubin, 1905	Eyes
Leachia eschscholtzii	Rathke, 1832; Chun, 1908	Eyes
Desmoteuthis pellucida	Chun, 1908	Eyes
Corynomma speculator	Chun, 1908	Eyes, mantle cavity
Crystalloteuthis glacialis	Chun, 1908	Eyes
Teuthowenia antarctica	Chun, 1908	Eyes
Toxeuma belone	Chun, 1908	Eyes?
Taonidium suhmi	Chun, 1908	Eyes
Bathothauma lyromma	Chun, 1908	Eyes

The organs are rarely distributed uniformly on the mantle surface and arms. I find in *Mastigoteuthis cordiformis* that the entire body is closely covered with conical papillae projecting from the skin; these, however, may not actually be luminous organs, since all the characterisitc accessory structures (described further on) are absent. In other forms a certain preference for the ventral surface is evident. Thus the organs may be restricted to the ventral arms (*Chiroteuthis*) or irregularly scattered in straight or oblique rows on the ventral side of the mantle, the funnel, the ventral side of the head and the ventral arms. If they are present in small numbers, the luminous organs are usually arranged symmetrically, although asymmetries may occur. Thus I find in *Calliteuthis* and *Histioteuthis* that the skin organs are well developed around the right eye, but absent or sparse at the left eye—a fact overlooked by earlier observers. A marked deviation from the preference for ventral surfaces is found in *Benthoteuthis*; they have 6 luminous organs on the base of the dorsal pairs of arms but none on the ventral arms.

In addition to these skin organs, many genera have characteristic **eye organs**, situated almost without exception on the ventral side of the eyeball. Their striking form already attracted the attention
41 of early authors. They were described for the Cranchiidae by Rathke (1832) and Grant (1833); among the Enoploteuthidae, Rüppell (1844) noted such structures in *Pyroteuthis margaritifera.* The genera *Thaumatolampas*, *Abraliopsis* and *Abralia* have 5 such organs on each side, *Enoploteuthis* about 10, *Pyroteuthis* 12, *Pterygioteuthis gemmata* 14 and *P. giardi* 15 organs at each eye.

Among the Cranchiidae, *Liocranchia* has 4 organs at each eye, *Leachia cyclura* 5, and *L. eschscholtzii* 8, and the genus *Cranchia* as many as 13 organs at each eye. In the stalk-eyed Cranchiidae, the ventral side of each eye bears 1–2 large, sickle-shaped organs.

The Histioteuthidae and Bathyteuthidae have no luminous organs on the eyes; nor are they present in Chiroteuthidae, by what has been reported so far. According to my findings, however, this family too has luminous organs on the eyes. Thus I found numerous luminous organs in 3 rows on the ventral side of the large eyeballs in a well-preserved, magnificent specimen of *Chiroteuthis imperator* from the Indian Ocean. Since Joubin did not mention luminous organs on the eyes in the closely related *Chiroteuthis picteti*, I examined the type specimens from the museum in Geneva for comparison (Plate XL, Figure 6) and indeed found in them luminous organs that are as distinct as those in our specimen. *Ch. picteti* has 24 luminous organs arranged in 3 rows. An exact count of the organs in *Chiroteuthis imperator* is difficult because of their tendency to become fused. I therefore examined the Mediterranean *Chiroteuthis veranyi* and found eye organs which were fused in two ventral longitudinal stripes and a few isolated organs between them (Plate XL, Figure 1). These organs must be very striking in the live animal, because they are distinctly visible through the gelatinous skin in the

preserved specimen. Unfailingly, Vérany illustrated these remarkable spots and stripes (1851, Plate XXIX).

Until recently, only the organs on the skin and those of the eyes were known. During the *Deep-Sea Expedition*, however, we found two new types of these organs. One or them, the **organs on the tentacles**, occurs in *Thaumatolampas* in small numbers (2 on each tentacle) embedded in the middle of the stalk. Troschel (1857) and Pfeffer (1884) described similar organs situated on the tentacle stalk of *Thelidioteuthis*, but not embedded in it.

The 4th type of luminous organs are those which I name "**ventral organs**". That they have been overlooked until now is mainly due to the fact that in the live animal they are visible only through the transparent abdominal wall, while in preserved specimens they are invisible from the outside. I found such organs in *Thaumatolampas* (1900, 1902); Hoyle (1902) described them in *Pyroteuthis*. *Thaumatolampas* has 8 such organs. Hoyle mentions 9 organs in *Pyroteuthis* but there are in fact 10, including a ventral organ on the pointed posterior end. Some of the ventral organs are the largest luminous organs known in the Cephalopoda and constitute a very significant and conspicuous feature, due to their
42 large size. The distribution of the ventral organs can be outlined as follows: two of them, the "anal organs", are situated close behind the anus, another two, the "branchial organs", are situated near the base of the gills, the other ventral organs are situated in the median plane if they are single, and distributed symmetrically between the gills and the anal organs if they number more than one.

These ventral organs were known so far in only two genera, *Thaumatolampas* and *Pyroteuthis*. I found, however, lentil-sized organs also in *Chiroteuthis imperator*, where they are situated on the ink sac. Microscopical study, furthermore, revealed similar organs in *Chiroteuthis veranyi* and proved that they resemble those on the ventral arms. It was, again, Vérany, who observed these large organs through the skin; he represented them as spots in his drawing (*loc. cit.*). Weiss (1888), who presented the first anatomical description of *Chiroteuthis*, did not overlook them either but he interpreted them as accessory nidamental glands.

I found ventral organs in only one genus of Cranchiidae—*Corynomma*, in which they are situated on the ink sac, as in *Chiroteuthis*.

Below, I present a general description of the **finer structure** of the luminous organs of the Cephalopoda. Details on these often very peculiar structures will be found in the special part of the book.

The **luminous body**, which is the main part of the luminous organ, varies in form. In *Thaumatolampas* (Plate IV, Figures 2, 6, 19), it consists of polyhedral or irregularly formed cells with distinct boundaries, spherical nuclei and distinct nucleoli. In the Cranchiidae these cells are also polyhedral or oblong-tubular and always distinct (*Cranchia*, Plate XV, Figure 9). They are surrounded by capillaries, and have a homogeneous or finely granulate and vacuolated content. In *Desmoteuthis* staining showed the presence of rod-like inclusions in the luminous cells (Plate XL, Figure 20).

However, the boundaries between the luminous cells are often less distinct. They are still recognizable in *Mastigoteuthis* (Plate XXXVII, Figures 2, 3), but have disappeared in *Pterygioteuthis* and *Chiroteuthis*, so that only the finely granulate cytoplasmic mass with scattered nuclei remains. In other forms, the cells form a fibrous tissue which finally comes to constitute the luminous body. This condition is indicated in *Thaumatolampas* (Plate IV, Figure 5) and is also recognizable in *Calliteuthis* (Plate XX, Figure 12). The cells here are radially arranged in the center of the organ and still have distinct boundaries between the cells at the widened base, where a large spherical nucleus is situated; the part near the center of the luminous body is divided into fibers which are held together by a hyaline substance.

The conditions are more complicated in *Abralia* and *Abraliopsis*. Joubin reported that the

43 luminous organ of *Abralia* contains a highly refractile, spherical central body with concentric striation. I found a similar structure in *Enoploteuthis*, whereas the corresponding body of an *Abralia* from the Indian Ocean consisted of two unequal, saddle-shaped halves crossing at a right angle. Similar formations exist in *Abraliopsis*. These are conspicuous by their sheen and of oval shape, surrounded by a plasmatic substance with numerous nuclei but, unlike the condition illustrated by Joubin for *Abralia*, without sharp outlines of the cells. I studied the embryology of these bodies—which resemble the "striated bodies" in the luminous organs of the Euphausiidae—in *Abraliopsis*. They develop from cells which become fused and lose their nuclei. This applies especially to the eye organs of *Abraliopsis*, while the nuclei of the skin organs are irregularly distributed in the vacuolated content of the fused cells.

In rare cases, the luminous organs consist entirely of luminous cells; one such case is the ventral organ on the tentacles of *Thaumatolampas*, in which only a slightly thickened capsule of connective tissue surrounds the large (nearly 2 mm long) luminous body which is situated in the center of the tentacle. A similar condition is present in both organs of *Mastigoteuthis glaukopsis*, which are embedded in gelatinous tissue.

In the great majority of cases, accessory structures are present next to the luminous organs. Of these, the **pigmented sheath** will be discussed first. This sheath is seldom absent or replaced by the pigment of the neighboring organs. I failed, however, to find a distinct pigmented sheath in the organs on the ink sac of *Chiroteuthis* and *Corynomma*, and in the eye organs of the Chiroteuthidae and Cranchiidae and in those of the genera *Thaumatolampas* and *Abraliopsis*. In the latter cases it is replaced by the pigment of the retina. If a pigment sheath is present, it is secreted either by nucleated pigment cells or, as Joubin described for *Abralia*, by chromatophores, which are sometimes arranged in definite numbers around the luminous organ (*Abraliopsis*). Since the organs cannot be rotated by muscles, the pigment-free zone of the organ indicates the direction in which the cone of light rays is emitted. The pigment is usually situated on the side facing the interior of the body; however, there
44 are interesting exceptions, as will be described elsewhere for *Mastigoteuthis*. In the concial anal organs of *Pterygioteuthis* and *Thaumatolampas*, the pigment is arranged so that the cone of light is emitted in the direction of the longitudinal axis of the organ toward funnel and head.

Often, an inner light-reflecting **tapetum** is situated in the pigmented ssheath; this is apparent already upon external examination, due to its strongly iridescent or nacreous sheen. In some cases the tapetum consists of polyhedral cells filled with highly refractile granules which cover the nuclei. In the anal organs of *Thaumatolampas* (Plate IV, Figures 9, 10), the tapetum forms a particularly deep layer.

In addition to these granulate cells, the fibrous tissues, too, may serve as reflectors. This is the case, for example, in *Abraliopsis* (Plate X, Figure 7), in which the organ contains reflectors between the luminous substance and the pigmented sheath, as in the Euphasiidae. The reflectors consist of concentric and partly parallel lamellae. Oblong nuclei are situated between the lamellae.

Finely fibrous reflectors are present in some organs of *Pterygioteuthis* (Plate XVI, Figures 5–9); they may be situated between the squamous cells described below (Plate XVI, Figures 1, 2, 10, 12, 13). The reflector of the large ventral organ of *Thaumatolampas* (Plate IV, Figure 16, *str.*) consists of similar finely fibrous tissue and so does that present in *Chiroteuthis* (Plate XLIV, Figures 1, 2), in which it is almost homogeneous at some points.

In connection with these fibrous systems, a group of cells has to be mentioned the function of which is not clear in all cases. These "**squamous cells**"—as I shall call them—were mentioned already by early observers; they are filled with a homogeneous content which is strongly refractile around the nucleus. In sections, they appear spindle shaped. The remainder of the cell is sometimes reduced to a thin envelope around the homogeneous content, while in other cases a large part of the cell is

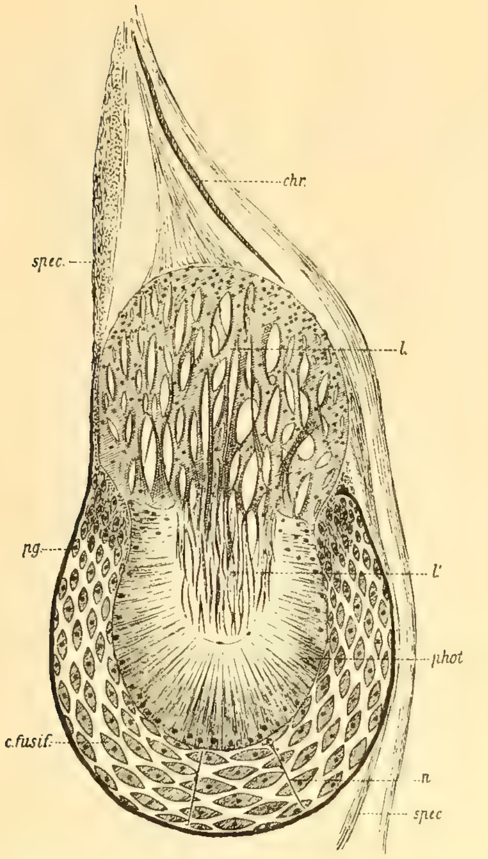

FIGURE 15. Longitudinal section of a luminous organ of *Calliteuthis hoylei* GOODR. Outer surface on the right:

phot. luminous body; *c.fusif.* spindle-shaped cells (reflector); *pg.* pigmented sheath; *l.* lens; *l'.* central part of lens; *n.* nerves; *spec.* mirror; *spec'.* distal part of mirror of the organ situated behind it; *chr.* chromatophores on outer surface of mirror.

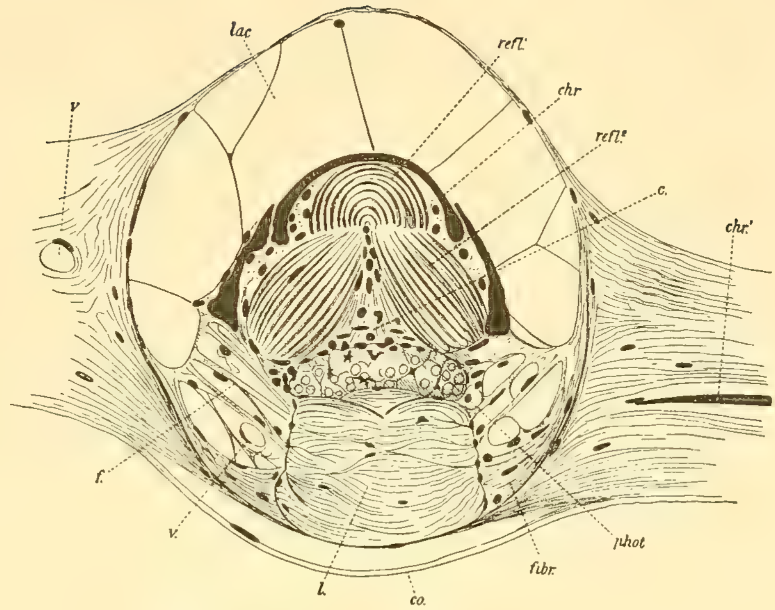

FIGURE 16. Section of an eye organ of *Abraliopsis morisii* VÉR.:

phot. luminous body; *c.* central cytoplasm with nuclei; *refl'.* central part of reflector; *chr.* pigmented sheath, consisting of chromatophores; *chr'.* skin chromatophores; *l.* lens; *lac.* lacunae surrounding the posterior and lateral parts of the organ; *f.* thicker fibers of the lateral wall; *fibr.* finer fibers reaching the lens; *v.* vessels; *co.* outer layer of skin (cornea).

separated from the refractile, strongly staining body and forms a differentiated polyhedral zone delimited from the adjacent cells (Plate IV, Figure 7). This homogeneous substance is often divided into lamellae (Plate IV, Figures 13).

The squamous cells function mainly as reflectors, e.g., in the Histioteuthidae, in which they are arranged in regularly intersecting curves between the luminous body and the pigmented sheath, as described already by JOUBIN (Plate XX, Figure 12). In other cases, they are situated on the outside of the luminous body, so that they would be able to function as a cornea or lens (*Thaumatolampas*, Plate IV, Figures 3, 9; *Pterygioteuthis*, Plate XVI, Figure 1). Finally, a few isolated squamous cells may penetrate into the luminous body (Plate XVI, Figures 1, 2, 3, 12); a compact layer of very large squamous cells divides the anal organ of *Pterygioteuthis* into an outer and an inner half (Plate XVI, Figure 12) which are held together by dish-shaped fibrous layers on the side walls of the organ. In all these cases it is difficult to determine the function of these cells in the absence of observation on the living organism. A very likely function will be discussed later in this description.

Some structures described above have to be interpreted as **lenses**. They are present in the eye organs of *Thaumatolampas* (Plate IV, Figure 3), *Abraliopsis* (Plate X, Figure 6), *Chiroteuthis* (Plate XLIV, Figure 6), in the stalk-eyed Cranchiidae (Plate XL, Figures 18–22) and in the ventral organs of *Thaumatolampas* (Plate IV, Figures 16–18) and *Pterygioteuthis* (Plate XVI, Figures 10, 11). The lenses consist in many cases of more or less long fibers which are sometimes bandlike and have a long central nucleus (Plate XLIV, Figures 6, 9). In the ventral organs of *Thaumatolampas* (not including the anal organs), these fibers form a large pad on the outer side of the organ; the fibers have a silky sheen and contain numerous nuclei. They are arranged in a dense, radial pattern and are so resistant that the microtome knife inevitably slips and tears the object.

In addition to these fine fibers, there are thicker masses of rod-shaped or meshed connective tissue
46 which may act as lenses. In *Calliteuthis* (Plate XX, Figure 12), the network consists of thick anastomosing fibers. Similar formations are found in the anal organ of *Pterygioteuthis* (Plate XVI, Figure 12).

Other formations of connective tissue act as a lens in *Abraliopsis*; they are fibrous in structure, with small, irregularly formed nuclei (Plate X, Figure 7). Since new luminous organs develop throughout life, it can occasionally be observed that the luminous body and the "anlage" of the lens form a central plug of cells which is characterized by large, oval nuclei. The cell material which develops into the lens has no distinct cell boundaries and later has pale nuclei between the branching, whorl-like fibers.

The dish-shaped organs of *Chiroteuthis* are filled with gelatinous tissue (Plate XLIV, Figures 1, 2). The lamellae are arranged like a honeycomb and the junctions at which they cross each other are filled with a homogeneous, gelatinous substance; these junctions sometimes have a gristly structure (Plate XLIV, Figure 4).

Various tissues may collectively form a lens. Thus, the lens of the anal organs of *Pterygioteuthis* consists of squamous cells, lateral systems of lamellae and a central system of rods. In some ophthalmic organs of the genus, the squamous cells are covered with large polyhedral cells having a partly homogeneous and partly granulate content (Plate XVI, Figure 2). The most original combination of different tissues in a lens is found in the posterior ventral organ of *Thaumatolampas*, in which the mantle musculature is thickened into a convex lens which is embedded in the large concave fibrous system of the organ (Text-Figure 20; Plate IV, Figure 16).

An accessory structure associated with the lens, found so far only in *Histioteuthis* and *Calliteuthis*, is a reflecting **mirror** in front of the luminous organ, always on its anterior part. This mirror, which was observed already by Vérany, is slightly parabolic and consists of thin fibers which pass on the inner surface of the luminous organ into the fibers of the upper cells of the lens, as described by Joubin for *Histioteuthis*. In *Calliteuthis*, the fibrous cords which form the mirror extend from one luminous organ to the other—from the inner side of the lower or posterior organ to the outer side of the upper or anterior organ.

Finally, it should be noted that the luminous organ is usually surrounded by a slightly denser connective tissue, which sometimes forms a capsule. But a main characteristic of the organs is their rich supply of blood vessels and nerves.

The **vascular supply** may be so rich that it attains a veritable network of capillaries in the luminous body (*Thaumatolampas*, Plate IV, Figure 19). The organs of *Chiroteuthis* have the most developed vascular system, with large afferent and efferent vessels which in the ventral and arm organs penetrate through the mesh of the gelatinous tissue and finally divide into a rich network of superfine capil-
47 laries. The walls of the capillaries are conspicuously thickened at their entrance into the luminous body and resemble gland tubules (Plate XLIV, Figures 3, 7, 8).

I was nearly always able to trace the **innervation** of the luminous body. Joubin and Hoyle found in *Histioteuthis* that the branches of their nerves, often accompanied by blood vessels, penetrate into the base of the organ, passing straight through the squamous cells of the reflector to reach the luminous body. I found finer fibers following a similar course in *Calliteuthis* and *Pterygioteuthis*. Hoyle noted such nerve fibers in *Pterygioteuthis*; I observed that these fibers pass through the squamous cells and can be followed to the terminal branches, as they turn black upon staining with iron hematoxylin (Plate XVI, Figures 15, 18). I found similar nerve fibers also in *Thaumatolampas*, in which they extend far into the luminous body, particularly in the anal organs. They are characterized by their straight course, divide repeatedly after entering the luminous body, and finally divide into very fine branches the ends of which are not recognizable (Plate IV, Figure 12).

Finally, an observation on the branchial organs of *Pterygioteuthis* and the anal organs of *Thaumatolampas*. The outer layer of the luminous body of these organs is covered with a granulate, finely fibrous layer of nerve tissue from which a large system of fibers radiates to the inner luminous body (Plate IV, Figure 14; Plate XVI, Figure 13).

The luminous organ may comprise **double organs**. This applies especially to the distal organ of the tentacles, the lateral organ of the eyes and the lateral ventral organ of *Thaumatolampas* (Plate IV, Figures 1, 3, 4, 18). The large branchial organ of *Pterygioteuthis* is also double (Plate XVI, Figure 13). It is not certain whether the two organs present in some Cranchiidae on the ventral surface of the eye are double. In *Desmoteuthis* (Plate LIV, Figures 7, 8; Plate LX, Figure 18) and *Taonidium* (Plate LIX, Figure 11), at any rate, these organs are partly fused.

As we have already seen, in several earlier instances, the luminous organs sometimes show differences in structure within the same species.

The condition in *Abraliopsis* (Figures 16, 17; Plate X, Figures 6, 7), in which luminous organs show marked differences, is an example of this **dimorphism of the luminous organs**.

The ophthalmic organs (Text-Figure 17) are flattened like a lens. They have no pigmented sheath
48 of chromatophores, no reflector, and the vacuoles in the skin organs are also absent. But above all they are characterized by an outer layer of radiating fibers, each of them with an elongate nucleus. The dimorphism of the organs of *Abraliopsis* is as strongly marked as that described by Hoyle (1902) for *Pyroteuthis*. In my earlier publications (1903), I already pointed out that the structure of the ventral organs, too, varies. Hoyle (1904) described a similar condition in *Pterygioteuthis*. Examination showed that the differences are much greater than was assumed. There thus exists a **polymorphism of the luminous organs** not known to such an extent in any other organism. Unique, however, is in this re-

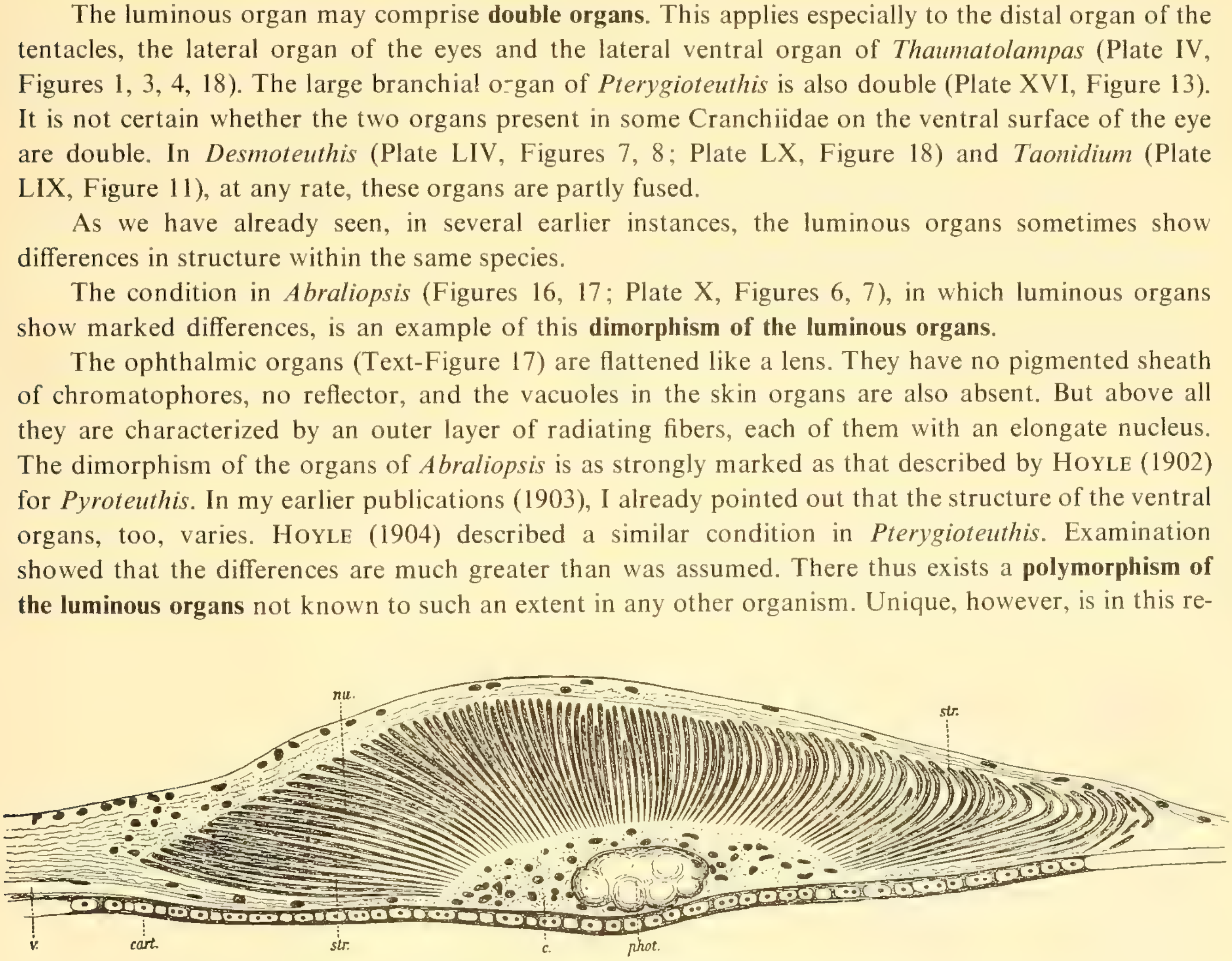

FIGURE 17. Longitudinal section of an eye organ of *Abraliopsis morisii* Vér.:

phot. homogeneous part of luminous body; *c.* cytoplasm of luminous body, with scattered nuclei; *str.* radial fibers (lens); *nu.* nuclei of radial fibers; *v.* vessel; *cart.* cartilage of eyeball.

spect the beautiful genus *Thaumatolampas*; I found that its 22 luminous organs are formed according to no less than 10 different structural principles. The organs of the tentacles are very large, oval, 2 mm long, and cause marked changes in the areas concerned. The nerve of the tentacle, which is normally round in cross section and situated centrally, is displaced to the periphery and compressed into a band; the muscles are also displaced to make room for this large formation, as shown in Text-Figure 18. The lower organ consists entirely of a large luminous body which consists of polyhedral cells; the upper organ (Plate IV, Figure 1) shows a surprising condition: a second organ is situated on the pigment-free central luminous body, slightly eccentric, and separated from the first organ by a dark-brown pigmented sheath. The luminous cells, which are characteristic for *Thaumatolampas*, are present in the center of the second organ and are covered posteriorly by a tapetum and on the outside by the fibrous radial system described above.

The 5 eye organs on the eye of *Thaumatolampas* are formed according to 3 different principles (Figure 19; Plate IV, Figure 3). The middle organ emits a bluish light, the 4 lateral organs have a nacreous sheen. The luminous bodies of the lateral organs (*phot. 4* and *5*) are arranged symmetrically to the middle organ. The organs adjacent to the middle organ have elongate luminous bodies covered by a hood of lens-shaped cells.

The luminous body extends to the surface on the side facing the blue organ and is covered here
49 only with a thin layer of ectoderm. The two outermost organs are similar, but longer and equipped with a separate, small organ situated at the distal lower margin and surrounded by a small circle of lens-shaped cells. The middle organ differs from the 4 lateral ones in the absence of a tapetum and in that the luminous substance is completely surrounded by squamous cells, as shown in the figure.

The organs of the tentacles and eyes thus show 5 structural principles. Similar differences are present also in the ventral organs. The anal organs (Plate IV, Figure 9) are covered on their exterior by lens-shaped cells and have a large reflector which consists mainly of granulate cells. The other ventral organs (Plate IV, Figures 16–18) always show a thick outer layer of silvery fibers. There are further differences, but these will not be described here; they involve the form and arrangement of the various layers.

This polymorphism is less marked in *Pterygioteuthis*. The luminous organs of this genus will elsewhere be described in detail; there are 7 types, including 4 in the eye organs alone. There are further differences in the branchial and anal organs (Plates XIV and XVI).

The different structural differences are listed below.

Monomorphic luminous organs		**Dimorphic organs**	
Thelidioteuthis	Skin organs	*Abraliopsis*	Skin and eye organs
Histioteuthis	,, ,,	*Enoploteuthis*	,, ,, ,, ,,
Calliteuthis	,, ,,	*Leachia*	Dimorphic eye organs
Mastigoteuthis	,, ,,	*Desmoteuthis*	,, ,, ,,
Cranchia	Eye organs (of different size, but of uniform structure)	*Crystalloteuthis*	,, ,, ,,
		Toxeuma	,, ,, ,,
Liocranchia	Eye organs	*Taonidium*	,, ,, ,,
Teuthowenia	,, ,,	*Corynomma*	Eye organs (?) and an organ on the ink sac
Bathothauma	,, ,,		

50 **Trimorphic organs**

Abralia	Skin organs and dimorphic eye organs
Chiroteuthis	Organs on ventral arms, eyes, ink sac

Polymorphic organs

Pyroteuthis	24 eye organs, 10 organs in the mantle cavity
Pterygioteuthis	28 or 30 eye organs, 8 organs in the mantle cavity (including 2 double ones). The organs are of 7 different types.
Thaumatolampas	4 organs on the tentacles (including 2 double ones), 10 eye organs (including 2 double ones), 8 organs in the mantle cavity (including 1 double organ). These 22 organs belong to 10 different types.

If we ask ourselves why there are 10 different structural types among only 22 luminous organs, we find that the only reasonable answer is that the light of the various organs differs apparently not only in intensity but also in quality. The most peculiar organs are those comprising 2 organs situated on top of each other. (If these double organs are taken into account, the total number of organs is 28). The intensity of the light is probably proportional to the size of the luminous body and to the extent to which it is equipped with reflectors and lenses. There are a number of accessory structures, in addition to those mentioned, which suggest that the **color of the light** is also different. In the live animal, the middle organs of the eye emit a magnificent ultramarine-blue light, the middle of the 5 ventral organs shines sky-blue, and the two anal organs are ruby-red. The latter color is present even in preserved specimens. The middle eye organs of the living *Pterygioteuthis giardi*, too, are ultramarine-blue; here the coloration is caused by the squamous cells of the lens and seems mainly to be due to the thin lamellae. It is, however, not known to what extent the lamellae modify the light radiated by the luminous body from the posterior. It is possible that red and blue light is emitted, but the weak phosphorescence of some organs of *Thaumatolampas* permitted no distinction between different colors in the dark room. The observer who would be lucky enough to spot a living, healthy *Thaumatolampas* in all its magnificence would indeed behold a fairy-like sight.

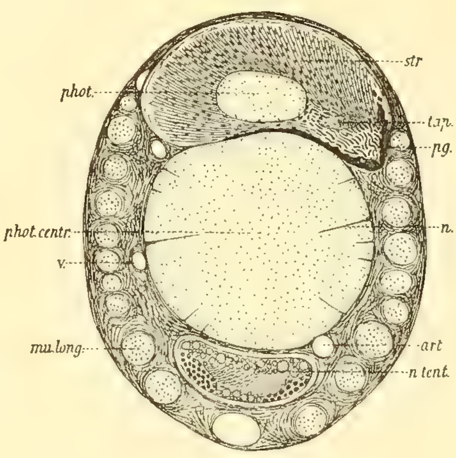

FIGURE 18. Cross section of tentacle of *Thaumatolampas diadema* CH., showing the double distal luminous organ:

phot.centr. large central organ; *phot.* luminous body of the peripheral organ with its fibrous radial system (*str.*), tapetum (*tap.*), and pigmented sheath (*pg.*); *n.* nerves of central organ; *n.tent.* nerve of tentacle; *mu.long.* longitudinal muscle; *art.* artery of tentacle; *v.* veins of tentacle.

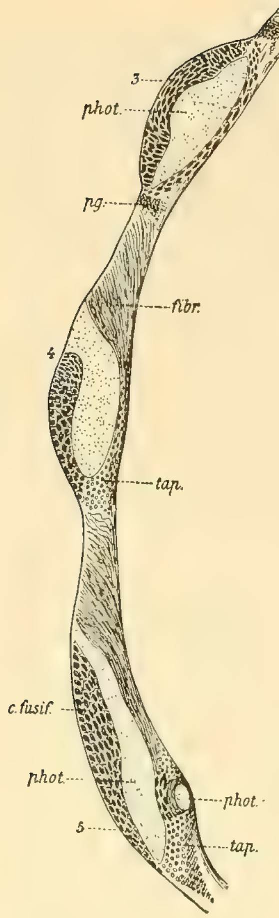

FIGURE 19. Longitudinal section through the middle (*3*) and both lower (*4* and *5*) eye organs of *Thaumatolampas diadema* Ch. Outer surface of the organs on the left:

phot. luminous body; *phot'.* small luminous organ situated below organ *5*; *c.fusif.* squamous cells; *tap.* tapetum; *pg.* pigment surrounding the middle organ *3*; *fibr.* fine fibrous cords.

But in other Cephalopoda, too, there are mechanisms that can only be connected with the function of producing colored light. In *Calliteuthis*, part of the light rays reflected by the mirror must be passing through chromatophores situated on the outside, in front of the mirror (Plate XX, Figure 12). A similar condition is present in *Mastigoteuthis*, in which the relatively few organs on the fins and on the ventral side
51 of the body are covered by a chromatophore filled with a pink pigment (Plate XXXVII, Figures 2, 3). Joubin (1893) named these organs "oeil thermoscopique", assuming that the chromatophore absorbs light from the outside but transmits heat rays, which are perceived by the large cells situated behind them; there is no experimental proof of this assumption. It would be just as reasonable to consider the whole integument of the Cephalopoda to be a filter which retains light rays, while heat rays are absorbed by heat-sensitive tissues. It would at least seem strange that *Mastigoteuthis* should be the only cephalopod, and even the only pelagic deep-sea animal, with such a sensitive deep-sea thermometer—absent in all other Cephalopoda.

The "oeil thermoscopique" is apparently a luminous organ which emits colored light through the colored disk above it—the pink chromatophore. As, according to Steinach (1901), the chromatophores react to the influence of strong light by expansion, it may be assumed that they also expand during the phosphorescence and function as a colored disc and not as an absorbing pigment sheath.

In conclusion, I would like to stress that a one-sided interpretation of the biological value of the luminous organs does not do justice to their importance for the organism. In most cases, the organs probably serve as a lure for the prey. At the same time, their characteristic distribution on the body

certainly creates a pattern which facilitates recognition of the sexes. BRAUER attempted an interpretation to this effect of the presence of luminous organs in deep-sea fishes. Should it be confirmed that these organs emit colored light, then the phenomenon can indeed only be interpreted as a mechanism for the recognition of the sexes in the dark depths.

Finally, some remarks on the **development of the luminous organs**. In the Cranchiidae, the luminous body passes so imperceptibly into the surrounding ectodermal cells (Plate LX, Figures 1–3), that it would be hard not to conclude that it actually develops from them. It apparently emerges from a thickening of the ectoderm which causes an invagination. This is suggested by a slit which often persists but which should not be interpreted as a glandular canal. A glandular character of the invaginated cells or a secretion from the thick pad of luminous cells has not been demonstrated. It is strange, however, that capillaries are abundant in the luminous body whereas they have never been observed in the ectoderm.

I failed however to discover any relationship between the ectoderm and developing luminous organs in larvae of other Cephalopoda or in those Enoploteuthidae (*Abraliopsis*, *Enoploteuthis*), in which throughout life new luminous organs are formed between the already existing ones. The earliest "anlagen" of luminous organs are here clusters of cells in the cutis which apparently belong to the connective tissue, i.e. the mesoderm.

52 # Special Part

Oegopsida libera CHUN

Funnel apparatus free; ventral wall of funnel, collaris and depressor muscles not fused with the mantle. Funnel valve present.

Teuthidae VERRILL 1881

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1. Family **Enoploteuthidae** PFEFFER

The family **Enoploteuthidae** was established by PFEFFER (1900, pp. 152 and 163). Its representatives were previously placed in the family Onychoteuthidae established by GRAY (1847, p. 206; 1849, p. 45). According to GRAY, the Onychoteuthidae comprise those forms the arms and tentacles of which bear hooks as well as those the arms of which bear suckers and the tentacles of which bear hooks, and, finally, the genus *Ommatostrephes* which has only suckers. STEENSTRUP (1861), realizing that this group is heterogeneous, restricted the definition of the Onychoteuthidae to a family he named "Onychii". He gave no precise diagnosis for this, nor the other families established at that time. However, the composition of the Onychii can be obtained from HOYLE (1886, p. 37), who included the genera *Enoploteuthis*, *Cucioteuthis*, *Ancistrocheirus*, *Abralia*, *Veranya*, *Onychoteuthis*, *Ancistroteuthis*, *Teleoteuthis* and *Gonatus*. Later authors, excluding VERRILL, accepted the family Onychii, and even now it is still maintained by FISCHER and JOUBIN (1906, p. 334).

The forms placed in the Onychii are hook-bearing Oegopsida which HOYLE divided into the two subfamilies Onychoteuthidae and Gonatidae. VERRILL (1881, p. 427) did not accept the name Onychii, and placed these forms in the family Teuthidae, a name established by OWEN in 1838 and accepted also by FÉRUSSAC and D'ORBIGNY (1835–48, *Introduction*, p. XXXVII). However, the Teuthidae as understood by Verrill are not identical with those of OWEN, FÉRUSSAC and D'ORBIGNY.

53 PFEFFER (1900) fortunately divided the Onychii into the families Enoploteuthidae and Onychoteuthidae.

The main differences between these two families, according to PFEFFER's diagnosis, are in the structure of the gladius. These differences are not significant and consist mainly in that in the Onychoteuthidae, there is a solid, pointed tip on the end of the gladius, which comprises a process of the dorsal keel. Another character was already used by GRAY: he divided the genera of his Onychoteuthidae into those which have hooks on the tentacles as well as arms (Enoploteuthidae) and those which have

hooks only on the tentacle clubs (Onychoteuthidae). The occurrence of hooks, of course, does not exclude a simultaneous occurrence of some suckers persisting on the arms or tentacle club which were not transformed into hooks.

These differences between the two families are small. However, I recognize the **Enoploteuthidae** as a separate family mainly because of another character which I consider as much more significant and also as proof for the primitive character of the Enoploteuthidae: **The buccal funnel of the Enoploteuthidae is supported by 8 pillars and ends in 8 points**, while that of the Onychoteuthidae has only 7 pillars and 7 points. In addition, the 4th arms have ventral attachments in the Onychoteuthidae but dorsal attachments in the Enoploteuthidae (Figure 8, p. 16).

The 8-radiate structure of the buccal funnel represents, in my opinion, the primitive condition from which the 7- or 6-radiate condition in the other Oegopsida developed secondarily. The latter condition developed by fusion of the two dorsal pillars, the unpaired attachments of which then branch and pass into the two margins on the basal dorsal surface of the dorsal arms. In the Enoploteuthidae, an indication of this condition is present in the genera *Pterygioteuthis* and *Pyroteuthis*, in which the dorsal pillars are closely continuous but still separate, especially in younger specimens.

The new genus *Thaumatolampas* resembles the Enoploteuthidae in the structure of the buccal funnel, but differs from all other Enoploteuthidae in showing no trace of transformation of suckers into hooks on the arms or tentacle clubs. Anyone considering this character as very important, like the earlier systematists, will not be inclined to place *Thaumatolampas* in the Enoploteuthidae. I, too, had for this reason established the family Thaumatolampadidae (1903, p. 68) for the genus *Thaumatolampas*, which is furthermore characterized by the presence of luminous organs on the tentacle stalks. Since, however, except for the absence of hooks, *Thaumatolampas* shows all the characters of the Enoploteuthidae, I propose to divide the Enoploteuthidae into two subfamilies: the **Thaumatolampadinae** and **Enoploteuthinae.**

54 **Diagnosis of the Enoploteuthidae:**

Buccal funnel with 8 pillars and 8 points; dorsal pillars rarely contiguous (Pterygiomorphae). The attachments originating from the pillars are dorsal on the 1st, 2nd and 4th arms, ventral on the 3rd arms. Arms and tentacles with suckers, which rarely persist throughout life but are usually partly transformed into hooks either only on the arms (*Pterygioteuthis*) or on the arms and tentacle stalks. Gladius feather-shaped, consisting of a rhachis and a narrow, rooflike vane which ends posteriorly in the form of a spoon without forming a cone. Luminous organs present on the body.

The **luminous organs** are characteristic for the family; they are usually dimorphic, but often polymorphic. They form 4 types: **skin, eye, tentacle** and **ventral organs**.

Luminous organs situated inside the tentacle stalk are present only in *Thaumatolampas*, which is unique among all Oegopsida in this respect.

The eye organs are apparently present in all species. They are always situated on the ventral side of the eyeball and form a single row or are irregularly distributed.

The skin organs are situated on the ventral side of the mantle, funnel, head and arms; only a few are present on the dorsal surface.

In some genera, e.g. *Ancistrocheirus*, the skin organs are apparently restricted to the mantle, where they are very large. The smaller organs usually form dense groups, but they are sometimes arranged in more or less distinct longitudinal rows which are present also on the head and on the arms.

Ventral organs are known in only 3 genera : *Thaumatolampas*, *Pyroteuthis* and *Pterygioteuthis*.

They are polymorphic and may be divided into anal, branchial and abdominal organs. They were observed already by the *Valdivia* expedition because they shine distinctly through the semitransparent skin of freshly caught specimens. In preserved specimens these organs become visible only after opening of the mantle cavity, which may explain why they have been overlooked in the past. Hoyle (1902, 1904) described such organs in the genus *Pyroteuthis*, no specimen of which was caught by us; in greater detail he described the ventral organs of *Pterygioteuthis*.

Ventral and skin organs are never found together.

The luminous organs thus provide important and striking characters for the systematic distinction of genera and species.

55 Another important systematic character is the form of the **posterior end of the body**, which is either level with the posterior margin of the fins or projects more or less beyond them. The latter applies especially to *Ancistrocheirus* and *Enoploteuthis*, in which the posterior end has a gelatinous consistency. In *Pterygioteuthis* and *Pyroteuthis*, the posterior end is conical and projects beyond the fins as a sharp prominent spine.

Other systematic characters are only incompletely known. This applies particularly to the **hectocotylization**. The only information available on hectocotylization in the Enoploteuthidae consists in the old data of Claus (1858, p. 257, Plate 10). He showed that in *Abralia* the left ventral arm, and in *Pyroteuthis* right ventral arm was hectocotylized. I observed hectocotylization in two other genera, both cases involving the left ventral arm. In *Abraliopsis*, as described also by Hoyle (1904), it includes the formation of a wide ventral protective membrane; in *Pterygioteuthis* the arm undergoes marked changes: loss of suckers or hooks and formation of large glandular pads between which occur chitinous plates with spines or hooks. Although as far as is known today, hectocotylization is restricted to the ventral arms, it is remarkable that in genera as closely related as *Pyroteuthis* and *Pterygioteuthis*, the right ventral arm is modified in one case and the left one in the other.

Little is known so far on the systematic importance of the internal organs. Some data are given below, but they are too fragmentary to permit the drawing of conclusions bearing on the relationships between the different forms. Only certain characters, mainly of the morphology of the **female genitalia**, could be used in systematics. Thus of all the Oegopsida, only two genera of Enoploteuthidae, *Abralia* and *Abraliopsis*, have no nidamental glands; this absence is compensated by a particularly strong development of the oviduct glands, even to the extent of contiguousness in their middle in mature animals. According to Brock (1880, p. 77), the same applies to *Enoploteuthis*.

On the other hand, I found large nidamental glands in *Thaumatolampas*, *Pterygioteuthis* and *Pyroteuthis*. A peculiarity of *Pterygioteuthis* was that only the left oviduct was developed in the 3 families examined.

Octopodoteuthis (*Veranya*) differs in many respects from the general character of the Enoploteuthidae. Pfeffer (1900) placed this genus in the Enoploteuthidae, although it differs in the form of the buccal funnel and arm apparatus. I consider it as the representative of a separate family, as will be discussed below.

56 In the systematic review of the Enoploteuthidae presented below, the genus *Cucioteuthis* is not included, since—despite the description of fragments by Joubin (1900, p. 51ff.)—this genus is so incompletely known as yet that I cannot decide whether it belongs to the Enoploteuthidae or to the Onychoteuthidae.

Finally I wish to note that I consider the genera *Compsoteuthis* and *Micrabralia*, established by Pfeffer, to be juvenile forms of *Abraliopsis* and *Abralia* respectively; further details will be given in the description of the postembryonic development of this genus.

The diagnosis of *Ancistrocheirus* is based on data of PFEFFER and HOYLE (1905), since I did not examine this genus.

Enoploteuthidae

Subfamily I

Thaumatolampadinae

Arms and tentacle clubs with suckers only.

Buccal funnel 8-radiate, free. Fins broad, less than half the mantle length, level with posterior end of body. Luminous organs polymorphic; 5 eye organs arranged in a row; 2 organs on the tentacle stalk; up to 8 ventral organs in the mantle cavity. Nidamental glands present.
Thaumatolampas CHUN

Subfamily II

Enoploteuthinae

Suckers of arms and usually of the tentacle clubs transformed into hooks to a varying extent.

Tribe I

Enoplomorphae

Buccal funnel free; dorsal buccal pillars separate. Luminous organs more or less numerous on ventral outer surface of body; eye organs uniserial. Ventral organs in mantle cavity absent.

Fins ending at level of posterior end of body

57 Fins slightly longer than half the mantle, tapering strongly posteriorly. Buccal funnel wine red. Arms with 2 rows of hooks, with suckers at the tip. Ventral arms with pointed tip. Ventral row of suckers suppressed in proximal hand part of tentacle club. Ventral median row consisting of 4 hooks; dorsal median and marginal row consisting of 4 suckers each. Left ventral arm hectocotylized with moderately developed protective membranes and glandular swellings near the tip. Luminous organs on ventral side of mantle dense and diffusely distributed. Eye organs dimorphic, 5 in a row on each side; marginal organs very large. Nidamental glands absent.
Abralia GRAY

Fins, longer than half the mantle, tapering strongly posteriorly. Buccal funnel dark violet. Arms with 2 rows of hooks, with suckers at tip; ventral arms

Fins ending at level of posterior end of body

ending in 3 knoblike swellings. Proximal hand part of tentacle club with at most 8 hooks in 2 rows, developed by transformation of suckers of the median rows; medioventral hooks larger than mediodorsal hooks; ventral marginal row of suckers suppressed. Left ventral arm hectocotylized with very wide ventral protective margin without glandular swellings. Luminous organs of ventral side of mantle dense, sometimes arranged in indistinct longitudinal rows. Eye organs 5 in a row on each side; marginal organs slightly larger. Nidamental glands absent.

Abraliopsis JOUBIN

Fins two-thirds of mantle length, broader at posterior end of body. Arms with 2 rows of hooks, with suckers at the tip; ventral arms shorter than the other arms. Proximal hand part of tentacle club with 2 rows of numerous hooks formed by transformation of suckers of the median rows; juvenile forms with 2 marginal rows of large suckers and 2 median rows of small suckers. Luminous organs on ventral side, head and on tentacle stalk not numerous.

Thelidioteuthis PFEFFER

58 Posterior end of body projecting beyond fins

Posterior end of body gelatinous. Fins half as long as mantle. Arms with 2 rows of hooks, with suckers at the tip. Both marginal rows of proximal hand part of tentacle club suppressed; medioventral row consisting of about 7 large hooks, mediodorsal row with about 7 smaller hooks. Luminous organs on ventral side of mantle, head and arms arranged in longitudinal rows. Eye organs about 10 in a row on each side, marginal organs slightly larger.

Enoploteuthis D'ORBIGNY

Fins large and wide, extending almost to anterior margin of mantle. Arms with biserial hooks with suckers at the tip. Both marginal rows of proximal hand part of tentacle club suppressed; medioventral row consisting of about 9 large hooks, mediodorsal row with about 9 smaller hooks. Luminous organs large, in small numbers on ventral side of mantle.

Ancistrocheirus GRAY

Tribe II

Pterygomorphae

Buccal funnel fused with sail-like protective membranes of base of arms; dorsal buccal pillars situated close together, fused at the base. Luminous organs on ventral surface of body absent; eye organs irregularly distributed on ventral side of eyeball; polymorphic ventral organs present in mantle cavity. Posterior end of body pointed, projecting beyond fins. Tentacles with a spindle-shaped swelling at the base. Nidamental glands present.

A few median suckers on the arms transformed into hooks: this transformation affects either one or both ventral rows. Tentacle club with suckers only. Left ventral arm hectocotylized *Pterygioteuthis* FISCHER

Arms with 2 rows of hooks, with suckers at tip of 1st, 2nd and 3rd arms. A few suckers of ventral median row of hand part of tentacle club transformed into hooks. Right ventral arm hectocotylized. *Pyroteuthis* HOYLE

59

1. Subfamily: *Thaumatolampadinae* CHUN

Thaumatolampas CHUN

Thaumatolampas diadema CHUN
(Plates I–IV)

Enoploteuthis diadema CHUN, 1900, p. 532 Fig.
? *Lycoteuthis jattai* PFEFFER, 1900, p. 161.
Lycoteuthis diadema CHUN, 1902, pp. 569, 570 Fig.
Thaumatolampas diadema CHUN, 1903, p. 67 ff.
Lycoteuthis diadema PFEFFER, 1908, p. 294.

Localities: Station 89: southern part of Benguela Current, 31°21′S, 15°58″E—One female. Vertical net to 3,000 m.
Station 118: West Wind Drift, 40°31′ S, 15°6′ E—One female. Vertical net to 1,500 m.

I designate this magnificent South Atlantic species as type of the new genus *Thaumatolampas*. I do not agree with Prof. PFEFFER—to whom I sent all Cephalopoda collected by the *Valdivia* for examination, including the 2 specimens of *Thaumatolampas* mentioned above—that these specimens belong to the genus *Lycoteuthis* described by him (PFEFFER, 1900, p. 156). He recently attempted to justify this view in detail (PFEFFER, 1908, p. 294). But his arguments do not convince me of the identity of the two genera or that they belong to the Onychoteuthidae.

PFEFFER based his diagnosis on two specimens from the stomach of a dolphin the suckers of which were completely lost. He described them as follows: "Posterior end of gladius very short and thick, compressed; spoon very large, keel not visible through dorsal skin; protective membranes of arms with strongly developed transverse bridges; tentacles with 4 rows of hooks; buccal membrane dark, with 8 points and attachments and with only 2 pores."

He states on p. 161: "The hooks of the tentacles are lost. However, the form of the soft parts of the suckers proves that hooks had been present."

The tentacle clubs of my specimens, which are well preserved, bear 4 rows of suckers which show no trace of transformation into hooks. (Considering the size and the relatively far advanced development of the organism, such a transformation should have taken place long ago.) I therefore cannot accept the two genera as identical.

60 PFEFFER states further (1908, p. 294): "I considered *Lycoteuthis* as belonging to the Onychoteuthidae; the structure of the gladius certainly places this genus in the Onychoteuthidae, also the formation of the funnel cartilage the basal part of which projects anteriorly beyond the free cartilage, which is very

characteristic for the Onychoteuthidae. On the other hand, *Lycoteuthis* is clearly an aberrant form; the isolation of this genus from most other Onychoteuthidae is strengthened by the formation of the luminous organs which I did not examine in 1900. It would therefore be preferable to designate the genus as type of the subfamily Lycoteuthinae, of the family Onychoteuthidae."

The gladius of my specimens did not show the characters of the Onychoteuthidae which PFEFFER (1900, p. 155) described as follows: "the keel always continues beyond the terminal cone as a solid, usually long point situated more or less obliquely on the cone." The gladius of *Thaumatolampas* (Plate III, Figures 6–8) ends in a broad spoon which is not laterally compressed and bears no oblique point.

On the other hand, both genera show a character which is present only in the Enoploteuthidae, a buccal funnel with 8 points. In addition, the ventral arms of *Thaumatolampas* are attached dorsally as in the Enoploteuthidae (not ventrally as in the Onychoteuthidae). This character indicates clearly that *Thaumatolampas* belongs to the Enoploteuthidae.

I considered the presence of luminous organs in the mantle cavity as a further character of the Enoploteuthidae. However, this character loses its systematic value following the recent discovery of such organs in *Onychoteuthis banksi* (HOYLE, 1907, p. 14).

Form of body

The **body** is vase-shaped with relatively large fins which form a rhombus. The large eyes do not project, and the arms and tentacles are moderately long. The luminous organs of the live animal have a nacreous sheen and some organs show a ruby red or blue iridescence. The body is fleshy and partly transparent, so that the ventral organs are distinctly visible through the mantle. The luminous organs of preserved specimens are recognizable only after opening of the mantle cavity.

The **mantle** is fleshy, and has a dorsal length of 80 mm in the larger specimen. Its dorsal surface descends gradually toward the posterior end of the body. The mantle margin forms a blunt dorsal corner and two indistinct ventral corners; the indentation between the ventral corners is weakly marked.

The **fins** are triangular and well developed; both fins together are 28 mm wide. Their dorsal bases are approximated and are 14 mm long in the larger specimen. Their slightly curved anterior margin extends perpendicularly to the longitudinal axis of the body, the posterior margin extends obliquely to the posterior end of the body without projecting beyond it.

61 The **gladius** (Plate III, Figures 6, 7, 8) is narrow and resembles that of the Enoploteuthidae. The rhachis widens only slightly anteriorly and bears 3 anterior ridges. The vane is only weakly developed, slightly widened in the middle of the gladius, tapering in the posterior quarter and ending in a wide, spoon-shaped terminal cone (Figure 8).

The **funnel** is of normal form and projects to about the posterior third of the eyes. The funnel groove is weakly developed and contains 2 strong adductors which form a plate on each side and are not divided. Funnel valve and funnel organ are well developed (Plate II, Figure 4). The funnel organ consists of 2 large oval ventral plates and a single dorsal part which ends anteriorly in a broad apex and is divided posteriorly into two lobes by a deep slit. The oblong funnel cartilage (Plate II, Figure 3; Text Figure 20) is 6.5 mm long; it tapers anteriorly and is obliquely truncate posteriorly; it has a narrow groove which extends obliquely to the m. collaris into which fits the mantle cartilage which is 7 mm long. The musculus collaris (Text Figure 20) extends broadly to the neck cartilage, which is widened anteriorly like a spatula and has a simple, shallow groove (Plate III, Figure 9). The corresponding dorsal mantle cartilage has parallel margins and a simple median ridge.

The **head** is 13 mm wide (measured between the outer margin of the two lenses). The large, not markedly projecting eyes have a weakly developed anterior sinus (Plate II, Figure 2). The interior of the eye of the live animal was black.

There are 3 moderately developed cephalic (nuchal) folds which project anteriorly. The median fold bears a well-developed olfactory tubercle (Plate II, Figure 2). The folds are connected by a small transverse bridge which delimits a short neck area extending to the m. collaris.

The **arms** (Plate III, Figure 1) are moderately large and arms and tentacles bear only suckers. As noted above (p. 48) this is one of the important characters of the subfamily.

The arms are of about equal length, formula: 2, 4, 3, 1. However, this applies only to the specimen from Station 89, which is the larger of the two, and in which the 2nd and 1st arms are 14.5 and 12 mm long. In the smaller specimen, the 1st, 3rd and 4th arms are about equally long; the formula is 2, 3, 4, 1.

The swimming membrane of the 1st arms forms a weak keel which extends to the base. The ventral protective membrane is strongly developed; the first arm bears 24 pairs of suckers, including 12 pairs of small suckers at the tip which decrease gradually in size.

The 2nd arms are the longest and bear 26 pairs of suckers, of which the 6 pairs at the tip are very small. The ventral protective membrane is well developed.

The 3rd arms are not the longest, but they are the strongest and have a large protective membrane on
62 the ventral side, with distinct transverse muscular bridges like the membranes of the 2nd arms. The 3rd arms bear 24 pairs of suckers, of which the 6 distal pairs are very small. The well-developed swimming keels of these arms form high, sickle-shaped keels their whole length.

The 4th arms have ventral protective membranes which are as small as the dorsal membranes. The swimming keels are well developed, but not as strongly as those on the 3rd arms. They extend broadly onto the basal part of the 3rd arms. The ventral arms bear about 30 pairs of suckers, of which the 6 distal pairs are very small.

The **tentacles** (those of the larger specimen are shown in Plate III, Figure 1) are moderately long and nearly round in cross section. The club is slightly but distinctly wider than the stalk. Each tentacle bears 2 large, embedded luminous organs which will be described in detail below. Luminous organs on the tentacles have not been found in any other Oegopsida. The tentacle is attached at the base by a long, narrow ventral muscle.

The tentacle club (Plate III, Figure 2) is curved dorsally like a chamois horn and bears 2 distinct protective membranes with transverse muscular bridges. There is a high, keel-shaped swimming membrane which is situated slightly dorsally on the distal part of the club. The sucker-bearing surface is flat and is divided into a carpal part and a large hand part. The carpal part bears 5 suckers, and a few indistinct knobs between them. The hand part is covered with suckers arranged in very regular rows of 4 to the tip of the club, where suckers are barely visible even with a strong magnifying lens. Characteristic for *Thaumatolampas* is the presence of very large, contiguous suckers on the proximal part of the club, mainly in the 3rd–6th oblique rows. The club of the large specimen is 6 mm long.

The **suckers** (Plate III, Figures 10–14) usually show the characters typical for all Oegopsida; on the arms they form two alternating rows which are separated by the bases of the muscular bridges of the protective membranes. The stalk of the sucker (*ped.*) enters a well-developed muscular pad (*p.*) which activates suction. The chitinous cup (Figure 11, *ch.*) is rather thick and is secreted by a distinctly translucent matrix (*ma.*). Its proximal wall (i.e. that facing the base of the arm) is narrower than the slightly concave distal wall. The outer margin of the cup consists of a radially striated ring (*ann.*) which is particularly well developed on the suckers of the club (Figure 12); then follows a middle part with 3 levels of teeth situated on polyhedral chitinous plates, as already described by Niemec (1885, Plate 4) for the suckers

of Decapoda. The teeth of the two upper rows (*d.'*) are obliquely edged on the suckers of the arms
63 (Figures 10, 11); they are widened on the tentacles (Figure 14) like a spoon and have radial thickenings toward the tip. Those of the lower (inner) row are true teeth (*d.*), which gradually increase in size from the proximal margin toward the middle of the distal margin. The suckers of the tentacles have 8 or 9 teeth on each side (Figure 13), the suckers on the arms slightly fewer.

The **buccal membrane** is strongly developed and forms the buccal funnel with 8 points. It is deep violet in life (Plate II, Figure 6). The two dorsal points are situated close together between the first arms; the other points are situated about the level of the 2nd, 3rd and 4th arms. Eight strong, muscular buccal pillars extend to the points; they strengthen the outer wall of the buccal funnel and form the attachments of the arms. The pillars are more or less spindle-shaped, thicker in the middle from which extends the bundle of fibers which form the attachment. The manner of attachment is typical for the Enoploteuthidae: dorsally on the 1st and 2nd arms, ventrally on the 3rd and dorsally on the 4th arms (Plate III, Figure 1). The lower ends of the pillars are markedly narrowed and extend to the respective arms.

The outer wall of the buccal funnel between the 4th and 1st arms is covered with a fine membrane which extends from the attachment to the arms (Plate II, Figure 6). Between the other arms, a thin, transparent membrane at the base of the pillars and arms is only indicated. *Thaumatolampas* has 6 "pori aquiferi", if this term is used for the spaces between the buccal funnel and arms that are not covered with a membrane. The preserved buccal funnel showed the outer membrane of the proximal part to be thinner, revealing the chromatophores and pigmentation underneath it more distinctly.

The inner surface bears numerous villi which extend to the outer membrane of the lip (Text Figure 7, p. 14). This membrane is a narrow ring-shaped elevation separated by a groove from the thick inner membrane of the lip; the latter bears radial incisions (Plate III, Figures 1 and 16).

The structure of the buccal funnel is shown in the longitudinal section on Plate III, Figure 16. A large central nerve runs along the pillar, which consists mainly of longitudinal muscle fibers. Like the nerves of the arms, this nerve bears a thick layer of ganglion cells and sends fine fibers to the surrounding tissue. The layer of ganglion cells disappears at the narrowed, spindle-shaped proximal end of the pillar, and the nerve which is now relatively thin, extends in a curve toward the corresponding longitudinal nerves of the arm (Text Figure 7). Large chromatophores are situated between the nerves and the buccal villi and so are numerous vessels, including a larger vessel which apparently passes around the funnel. The villi contain an axis of gelatinous connective tissue to which thin bundles of muscle fibers extend. A thick glandular epithelium covers the villi. The cylindrical gland cells show the usual structure; they have a large vacuole filled with secretory granules. The vacuole takes up the entire distal part of the cell and often flattens the proximal nucleus. Between the glandular cells are
64 supporting cells which are wider at the surface and thin proximally. In addition, there are also reserve cells in the deeper layers. The glandular pad also extends on the inner and outer lips, but it becomes very flat on the outer lips. The epithelium is folded over at the edge of the inner lip and forms a matrix for the jaws. The lips consist mainly of gelatinous connective tissue with smooth muscle fibers.

The inner surface of the funnel is thus essentially a glandular layer which envelops the prey with a secretion before it passes to the jaws.

The buccal funnel bears a mysterious organ at the base of the 3rd buccal pillar. Already external examination (Plate II, Figures 6 and 7) shows knob-shaped thickenings (*s.*) the structure of which is recognizable in sections (Plate III, Figure 17). They show that the large longitudinal nerve of the buccal pillar enters the center of the knob. The nerve, which is still covered with ganglion cells, forms a loop in the knob, the recurrent proximal branch of which has lost the cover of ganglion cells and has become much thinner (Text Figure 7). The knob bears a thick vein on the outside which accompanies the nerve;

a much smaller arterial branch is situated nearby. A single layer of flattened epithelium covers the surface.

The function of this peculiar apparatus is not clear. Since a sensory epithelium is absent on the surface, the knob may be a sense organ for pressure. No such structure has ever been described in other Cephalopoda.

In addition to the attachments connected with the buccal pillars, there are the deep **attachments of the arms** which have not been described so far. In *Thaumatolampas* they fit the pattern described in the introduction inasmuch as a thick muscle extends from the ventral side of the base of each arm to the dorsal surface of the following arm. A broad ligament extends dorsally below this muscle to the ventral side of the adjacent arm (Plate II, Figure 7). The ventral ligaments of the 3rd arms are long; they are crossed below the ventral buccal pillar and then extend to the ventral arms (Plate II, Figure 6). The tentacles also have long muscular attachments (*funic. t.*) which are united into a single cord deep behind the ventral arm.

The **jaws** (Plate III, Figures 3–5) have the usual structure. The upper jaw of the smaller specimen (Figure 3) is 4 mm long and has a narrow rostrum which ends in the rostral wings (*a. r.*). Attached to the upper jaw are broad mostly transparent basal wings (*a. pal.*), the "palatine lamellae" of Steenstrup. The lower jaw shows no special characters either; like the upper jaw, it has distinct rostral wings and basal wings or "gular lamellae" (*a. gul.*).

65 The **radula** (Plate III, Figure 15) shows the simple structure which resembles that of other Enoploteuthidae. Each row consists of 7 teeth; there are median, lateral and marginal teeth. Since the lateral teeth adjacent to the marginal teeth are long and sword-shaped and resemble those adjacent to the median teeth, the formula according to Jatta is as follows:

3, 2, 2, 1, 2, 2, 3.

The apex of the median tooth projects beyond that of the two lateral teeth. The basal plates of the median teeth are oval, those of the lateral teeth are more or less square. Tooth-shaped processes at the base of the conical teeth are absent and not even indicated. The tooth plates of *Thaumatolampas* resemble those described by Hoyle for *Abraliopsis* (1904, p. 38, Plate VIII, Figure 9).

The **coloration** is yellowish on mantle, fins, funnel and tentacle club and purple on head and arms. Purple-red chromatophores are present everywhere, especially on the head and in the mediodorsal zone of the mantle. They cause the intensive purple color of the buccal funnel.

The stomach of both specimens is purple, the liver reddish-brown. The color is lost in preserved specimens. The color of the stomach may have been due to food remains.

The coloration of the live organism is dominated by the magnificent nacreous sheen of the luminous organs, some of which emit a sky-blue or ruby-red light.

Inner organs

Opening of the mantle cavity shows the strong funnel depressors (musculi depressores infundibuli) (Plate II, Figures 4, 5). They extend dorsally from the funnel cartilage into the funnel musculature, as shown in Text Figure 20; they then extend obliquely posteriorly and dorsally, and are united with 2 other muscles, the median shell muscle (musculus retractor capitis, according to Brock) and the strong and broad lateral retractor of the head (musculus retractor capitis lateralis). Two muscular cords which pass along the ventral abdominal wall extend from the dorsal wall of the funnel and are visible behind the funnel organ (Plate II, Figures 4, 5, *mu. r. abd.*); they are bordered on the right by the

vena cava, surround the rectum, then become narrower and pass dorsal to the median ventral luminous organ to the posterior ventral abdominal wall (Plate IV, Figure 18). Brock (1888, p. 22) named these muscles "median pallial adductor". I prefer the term "muscular rectus abdominis", because this muscle is not inserted in the membranous septum in the Oegopsida and hardly acts as a mantle retractor; it apparently functions as an abdominal constrictor, like the corresponding muscle of vertebrates.

The musculature of the abdominal wall partly covers the rectum, so that only its distal part is
66 visible. The anus is bordered by two liplike swellings and bears two well-developed anal appendages, each of which consists of two unusually wide lateral flaps of about equal size, supported by a muscular keel. Comparison with the drawings of the anal appendages of other Cephalopoda by Brock (1880, Plate XII) shows that the large size of the appendages of *Thaumatolampas* is the starting point for a series of changes the result of which in the Octopoda is that only the keel with weakly developed margin remains.

Only the stomach is visible through the abdominal wall. Opening of the abdomen shows that the stomach ends a short distance before the posterior luminous organ and that a shallow groove divides its thick-walled end part from the thin-walled anterior part into which the esophagus enters (Text Figure 20).

The caecum of the stomach is situated on the left side, almost at the level of the heart. It is more or less kidney-shaped and slightly laterally compressed; its hoodlike dorsal part is more transparent

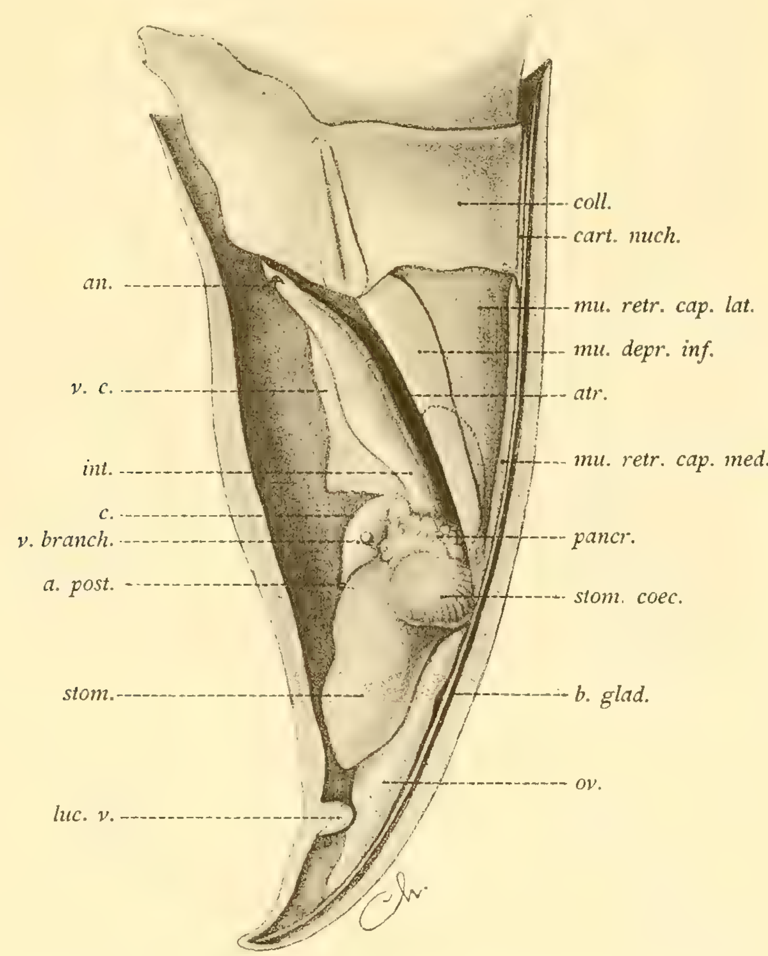

FIGURE 20. Longitudinal section of posterior half of body of *Thaumatolampas*:

an. anus; *a.post.* posterior artery; *atr.* ink sac; *b.glad.* shell sac; *cart.nuch.* neck cartilage; *coll.* collar; *c.* heart; *int.* intestine; *luc.v.* large ventral luminous organ; *mu.depr.inf.* funnel depressor; *mu.retr.cap.lat.* lateral retractor of head; *mu.retr.cap.med.* dorsal retractor of head; *ov.* ovary; *pancr.* pancreas; *stom.* stomach; *stom.coec.* caecum of stomach; *v.branch.* branchial vein; *v.c.* vena cava. The dotted line indicates the extent of the appendages of the pancreas.

than the ventral part. The spiral folds are distinctly visible dorsally; here they are slightly larger and not so dense as in the ventral part where they are indistinct.

The hepatic ducts are densely covered with pancreatic appendages and open in a knoblike elevation situated roughly in the middle of the anterior part of the caecum. The right duct surrounds the beginning of the mid-intestine and then unites with the left duct. The ducts extend far upward; the pancreatic lobes become larger and occupy a large area toward the liver (shown by a dotted line in Text Figure 20).

The hepatic ducts originate from the posterior surface of the oval liver, which is enclosed in an
67 iridescent envelope of connective tissue. The liver is covered dorsolaterally by the depressors and retractors of the head; it borders ventrally on the abdominal muscles. The liver lies almost exactly in the longitudinal axis of the body.

The stomach of the specimen from Station 118 was filled with legs of small Crustacea, shall fragments and partly violet soft parts, apparently belonging to Pteropoda.

Vascular system. The vena cava is visible on the right near the rectum (Plate II, Figures 4, 5, *v. c.*). The two branches of the vena cava with their venous appendages are also clearly visible through the ventral abdominal wall; they are shown in cross section on Plate IV, Figure 18. Removal of the ventral abdominal wall shows the swollen, anteriorly fingerlike venous appendages (Plate III, Figure 18). The mantle veins open behind the branchial heart into the venous appendages; the right mantle vein is shown in Figure 18 with its branches (*v. p. d.*). The figure also shows the large, oval branchial heart with its appendage and the delicate membrane which surrounds the coelomic area around the branchial heart.

The **gills** in the smaller specimen do not reach the posterior margin of the funnel (Plate II, Figure 3; Plate III, Figure 18), but in the larger specimen they do. The gills show the normal characters: the branchial ligament extends to the mantle (Plate III, Figure 18, *lig. br.*); the branchial gland is well developed and the branchial vein passes along the ventral margin and widens toward the atrium. Also typical is the spindle-shaped heart (Text Figure 20) the longitudinal axis of which is almost parallel to that of the body.

The single **renal sac** is distinctly visible anterior to the ventral luminous organs and opens on 2 oval papillae (Plate II, Figure 5) near the abdominal muscles. It has wide lateral diverticula below the luminous organs (Plate IV, Figure 18) which surround the lateral ventral organs and also the branchial organs on the dorsal side. The epithelium of the renal sac consists of thick, cubical cells with finely striated cytoplasm along the luminous organs (Plate IV, Figures 18 and 21); the nuclei of these cells are close to the surface, facing the luminous organ.

Genitalia. Both specimens are females. The ovaries are situated close to the dorsal wall of the stomach and are well developed also in the younger specimen (Text Figure 20). The posterior end of the ovary does not reach the posterior end of the body; opening of the mantle cavity shows that this part is situated above the stomach. The anterior end of the ovary extends to the caecum of the stomach. The ovary of the smaller specimen is 8 mm long and adheres so closely to the adjacent organs that the stomach and the large posterior luminous organ leave distinct imprints on it. The two oviducts are situated far from the ovaries. They are partly covered by the branchial hearts and the vessels which open into them (Plate III, Figure 18, *ovd.*). The right oviduct of the larger specimen (Plate III, Figure 19) is rather short and forms only 2 loops before it opens on a process, bordered by the base of the oviduct glands. Division of these glands into a transverse proximal part and two longitudinal lateral parts is still in-
68 complete. The distal part of the oviduct glands is very long in comparison with the short oviducts and ends in a narrow, slitlike opening.

Both specimens had well developed but small nidamental glands, widely separated behind the

branchial hearts (Plate II, Figure 5) and attached anteriorly by a delicate ligament which extends to the abdominal wall; the posterior end of the glands is embedded in the abdominal wall.

Luminous Organs

We were fascinated by the magnificent shine of the luminous organs of the live *Thaumatolampas*. The light from the tentacles, eyes and ventral side was so strong that we were able to take a photograph; Figure 1 of Plate II is based on this photograph. No other coloration known from deep-sea animals can be compared even remotely with the almost magic light of the luminous organs of *Thaumatolampas*. Its body appears to be covered with a diadem of precious stones. The middle organ of the eye shone ultramarine blue, the lateral organs with a nacreous sheen; the anterior organs of the ventral side shone ruby red, the posterior organs silvery white or with a nacreous sheen, except for the middle organ, which shone sky blue. A magnificent sight! After placing the specimen, which was already rather exhausted, in the dark room, I found that one of the organs emitted a bluish light. Lucky indeed is he who has seen the brilliance of a *Thaumatolampas*! It was the desire to investigate the structure of these organs in greater detail that moved me to embark on the study of Cephalopoda, resulting in this volume.

Arrangement of the Luminous Organs

Thaumatolampas has 22 luminous organs. It is the only known genus of Cephalopoda having luminous organs on the tentacles, each of which bears 2 organs. The proximal organs are situated above the base of the tentacle, the distal organ is situated just before the beginning of the club and shines through even in preserved material. The eye organs are situated along the ventral margin of the eye. There are 5 organs on each eye, arranged symmetrical to the middle organ; this symmetry is evident also in the finer structure of the organs. On the live *Thaumatolampas* we were able to demonstrate for the first time that luminous organs are situated also in the mantle cavity. In the mantle cavity of other genera of Enoploteuthidae luminous organs are also present. Earlier authors, however, overlooked them, mainly because the mantle becomes opaque after preservation. In the live animal, however, the mantle is transparent, so that the organs shine through. The presence of large luminous organs
69 on the ventral side of the mantle cavity is thus not surprising. Guided by our observations of the live *Thaumatolampas*, Hoyle later described similar organs in *Pterygioteuthis* and *Pyroteuthis*.

The organs of the mantle cavity (Plate II, Figure 3) consist of 2 anal organs, situated symmetrically behind the anus, and a crown of 5 ventral organs at the level of the base of the gills which, too, are arranged symmetrical to the middle organ. The latter organ is surrounded by the larger lateral ventral organs, which are situated near the branchial organs. The particularly large posterior ventral organ is situated near the posterior end of the body. It adheres closely to the inner surface of the musculature of the mantle which forms a lens-shaped thickening at this point (Text Figure 20). Prior to describing the structure of the different organs, a general review of the characteristic elements in the various organs, which show some peculiar features, is presented.

Comparative Description of the Luminous Organs
(Plate IV)

The **luminous cells** of *Thaumatolampas* are easily identified as the element which causes the emission of light. This applies particularly to the large proximal organ of the tentacles which consists almost

entirely of luminous cells in an envelope of connective tissue. The luminous cells are the only constant element in the varying structure of the luminous organs.

The luminous cells form a luminous body. However, they do not adhere closely to each other in all cases. There are often gaps between them which are partly filled by a network of capillaries. The cells vary in form. Their typical form in the center of the luminous body is shown in Figure 19. The outline of the cells has indentations into which fit processes of the adjacent cells. Other cells are tubular (Figure 6, central cells of the middle organ of the eye) or show transitions to spindle-shaped or cylindrical cells, some of them with a single process at one end, others with several processes at both ends. The latter condition (Figure 5) is common in the marginal parts of the middle organ of the eye. A distinctly differentiated membrane is not recognizable. Particularly characteristic for the luminous cells is their homogeneous cytoplasm which stains only weakly and is distinctly but not strongly refractile. Stronger staining is achieved when the cells are dying. This is shown in Figure 2 of the tentacle organ of the smaller specimen. The cells of the tentacle organ are already affected. The marginal cells appear as shown in the figure, while the central cells, to which the preservation fluid had not yet penetrated, had lost their sharp outline and showed a breakdown into droplets. This is a postmortem phenomenon, as shown by the luminous cells of the larger specimen which was preserved immediately and showed no trace of such a degeneration.

The nuclei of the luminous cells are spherical, rarely oval. They do not stain very intensively and have one or several nucleoli and usually a layer of chromatin granules on the nuclear membrane.

There are various accessory structures on the luminous body, e.g. the **pigmented sheath**. Many organs of *Thaumatolampas* lack such a sheath. Thus it is absent in the eye organs, in which it is apparently replaced by the eye pigment; nor is it present in the organs on the tentacles and in the ventral and branchial organs. Only the anal organs (Figure 9) are covered with a pigmented sheath, i.e. in the form of thin, pigmented flattened epithelium. The pigmented sheath is well developed in only one organ, which is situated on the central upper organ of the tentacles (Figure 1). Here it forms a readily visible layer of pigment particles comprising a cup-shaped layer on the inner surface of the organ and separating it from the large central organ of the tentacle.

A weak pigmentation is also present in the marginal organs of the eye, around the inner surface of the small organ that is situated below the large organ (Figure 4). On the other hand, the ring-shaped superficial pigment layer around the middle organ of the eye (Figure 6; Plate II, Figure 8) can hardly be considered as a distinct pigmented sheath.

A light-reflecting **tapetum** causes the nacreous sheen which is visible from the outside. The tapetum is most strongly developed in the anal organs, in which it is covered on the outside by the pigment layer (Figures 9, 10, 11). Here it is formed by several layers of polyhedral cells. The cells on the outer surface of this organ differ distinctly from those on the inner surface, not only in their structure but also in their staining properties. The cells of the inner surface stain well. Their nuclei are usually oval, sometimes bandlike or of irregular form; their cytoplasm is filled with numerous relatively large, strongly refractile granules (Figure 11). At the sharp, conical posterior end of the anal organ these cells are abruptly replaced by cells which form a thick layer on the outer surface of the anal organ (Figure 10). The latter cells are of irregular form, elongate, filled with strongly refractile flakes which are usually flattened into polyhedra by mutual pressure, so that the nucleus assumes an irregular form. Hemalum stains these cells pale yellowish, iron hematoxylin deep blackish blue, like the cells of the tapetum on the inner surface.

I found similar cells in the 4 lateral organs of the eye (Figures 3, 4, *tap.*). These cells, too, are filled with refractile granules (Figure 4) and have nuclei of irregular form.

Belonging probably also to the tapetum cells are some characteristic elements which I observed
71 in the lateral ventral organs, the branchial organ and the posterior ventral organ. They are situated behind the luminous body and differ in their slightly yellowish tone from the unstained organs (Figures 16, 17, 18). Sections show that they consist of elongate cells arranged in a single layer, their oval nuclei facing the luminous body; they, too, are filled with refractile granules. That half of the cells that has no nucleus is divided into fibers which combine with those of the adjacent cells into a thick, feltlike layer. In the lateral ventral organs, the cells of which are shown in Figure 20, this layer separates the small and the large luminous body (Figure 18).

The reflecting action of the tapetum is further enhanced by cells which consist of a number of lamellae. I found such cells between the luminous body and the tapetum of the anal organ (Figure 9, *lam.*). These cells form a thick layer on the outside of the tapetum and a thin layer on its inner layer. They comprise a system of lamellae with scattered rounded or oval nuclei, as shown in Figure 12.

Cells which I designate as "**squamous**" **cells** are an important but physiologically obscure element in the organs of the eyes and in the anal organs. These cells are almost always spindle-shaped in sections; their outline, however, rather resembles scales. These "squamous" cells always constitute several layers that form the boundary of the outer surface of the luminous body, but are sometimes present also on the inner surface. They may form densely compressed polyhedra (Figure 7), but sections show that they are more often spindle-shaped and thus swollen in the middle and flattened at the margin. They have a large, rounded or oval nucleus, usually with a large nucleolus. The cell content is always homogeneous, strongly refractile and easily stained. This substance sometimes fills the whole cell, leaving only a thin envelope around the refractile content. In other cases the condition is reversed. The central nucleus is never embedded in this refractile content but is instead surrounded by a light cell fluid which does not stain. In the eye organs, the nucleus is usually situated close to the refractile body or in a sharply delimited vacuole inside the refractile content. This is recognizable not only in sections (Figure 7) but also in surface views (Figure 8) of the squamous cells. Examination of the surface also shows that the refractile content has a sharp, often irregular outline at the periphery of the cell. In the anal organ, the refractile cell forms fibers (Figures 9 and 13); this may, however, be caused by preservation. However, there is often an extremely fine striation in that content that does not form fibers, suggesting that new layers are being successively formed on the old ones during the growth of the cell. The presence of fine
72 lamellae in this fibrous substance creates a magnificently iridescent pattern of colors. This will be referred to in detail in the description of the luminous organs of *Pterygioteuthis*.

It is difficult to give a satisfactory and general explanation of the physiological function of the squamous cells. Where they form a biconvex layer on the outer surface of the organ, they may be considered as a lens. This applies, for example, to the anal organs and to the marginal organs of the eye. The layer of squamous cells on the outer surface of the middle organs of the eye could also be regarded as a lens. A lens effect seems to be excluded, on the other hand, if the squamous cells are situated on the inner surface of the luminous body, as they are in the middle organ of the eye. Here the squamous cells apparently function as a reflector, as is the case in respect to the organs of the Histioteuthidae which will be described below.

Only observation of the live animal can show whether the squamous cells, particularly those in which the refractile content forms fibers, can give a different color to the light emitted by the luminous body.

The **fibrous cells** are another element of the luminous organs. They are present in the upper organ of the tentacle and form a thick layer, especially in the ventral and branchial organs. The fibrous cells are comprised of more or less long fibers, which sometimes form bands and have one or several elongate,

laterally situated nuclei (Figure 22). They radiate densely to the periphery of the organ and form an outer and an inner layer which envelop the luminous body completely. These cells cause the magnificent silky or nacreous sheen which is visible even in preserved material. Their resistance is so strong that the microtome blade inevitably slips and tears the material. The arrangement of these cells is best visible in whole cleared preparations like those in Figures 16 and 17. The inner layer of fibrous cells forms a regular radial pattern only in the immediate vicinity of the luminous body; it passes further on into a tissue formed of crossing fibers or a network of fibers of connective tissue.

The connective tissue around the organ is usually thickened and forms a more or less distinct envelope. This is well developed around the organs of the tentacles. It is also present at the organs of the eye, where it forms a thick layer of fine fibers which separates the organs. Similar layers of connective tissue surround the branchial organ and radiate from it as cords which pass through the diverticulum of the renal sac (Figure 17). These cords are covered with the thick epithelium described above.

In conclusion, it should be mentioned that the luminous organs have a rich supply of blood vessels and nerves.

The **vascular supply** takes place via the thicker vessels of the surrounding connective tissue. These vessels penetrate the various envelopes of the organ and form a dense **network of capillaries** inside
73 the luminous body. The capillaries surround the luminous cells and partly isolate them from each other. The dense capillary network is shown in Figure 19, which also shows the difference between the oval, finely granulate nuclei of the vessels and the rounded nuclei of the luminous cells which contain strongly refractile granules. Figure 6 shows a similar picture: a few luminous cells of the middle organ of the eye, surrounded by a network of capillaries.

The **innervation** of the luminous body, too, is clearly recognizable in preparations. The nerves which enter the luminous body are usually thicker if the luminous body is large. This is particularly true for the large organs of the tentacles and the large luminous bodies of the anal organs. In the latter, the nerves enter the organ from the outside, pass through the tapetum and the adjacent layer of lamellae and branch repeatedly between the luminous cells, as shown in the iron-hematoxylin preparation in Figure 12. The thinner branches are not visible, so that no end plates nor a network of the terminal branches are recognizable. The nerves sometimes contain elongate, finely granulate nuclei, resembling those constantly present in the thicker fibers which enter the envelope. A similar condition in the organ of the tentacles is shown in Figure 2. After passing the envelope of the organ, the thick nerves bend at a right angle and then branch repeatedly. The elongate, finely granulate nuclei of the nerve cells and the round nuclei of the luminous cells can easily be distinguished. The cells adjacent to the nerve are usually smaller than the other luminous cells, so that the nerve appears to be surrounded by a sheath of polyhedral cells.

In the anal organ, the nerves passing along the peripheral pad of squamous cells widen like an arcade on the inner surface of the pad (Figure 14) and form a nerve plate which creates a boundary between the luminous body and the squamous cells. Thinner fibers from this layer may penetrate independently into the luminous body. As the lower magnification in Figure 9 shows, this layer differs from the surrounding tissues in its large number of nuclei.

Description of the Luminous Organs

Tentacle organs. The presence of centrally situated luminous organs distinguishes *Thaumatolampas* from all other known Cephalopoda. Each tentacle bears 2 organs, of which the proximal, or lower organ, is situated about halfway along the tentacle and the distal, or upper organ, just before the carpal

part. The distal organ is double, i.e. it bears a second organ on the outer side of the tentacle which is separated from the central organ by a pigmented cup.

The proximal organ of the tentacles has the simplest structure. It consists only of an oval luminous
74 body, which is situated slightly eccentrically in the middle of the musculature. In the specimen from Station 118, this organ is 0.5–0.6 mm wide.

The distal organ of the tentacle (Plate IV, Figure 1) is double and resembles the proximal organ in that the main organ consists entirely of a luminous body and is situated in the center of the musculature. The distal organ is much larger than the proximal one; it is oval or sausage-shaped, 2.3 mm long and 0.7–0.8 mm wide. Its outer surface is slightly depressed by the outer organ. The large central organ, which consists entirely of a luminous body, markedly influences the topography of the tissue of the tentacle; the surrounding musculature is transformed into a sheath, and the nerve cord is displaced from the center to the inner surface of the tentacle. As shown in the figure, the blood vessels, too, are displaced toward the periphery. The luminous body is surrounded by a moderately thick sheath of connective tissue, through which enter numerous radial nerves which then divide into branches (Figure 2).

The peripheral organ situated on the central luminous body is 1 mm long and appears lens-shaped in longitudinal section. Its flattened surface facing the central organ is surrounded by pigment. The cross section in Figure 1 shows that the pigmented sheath passes on one side of the margin of the organ and forms an eccentric cup of pigment which was clearly visible in the live animal. The luminous body is oval and 0.25 mm long. A group of cells situated near the pigmented cup acts as a tapetum (*tap.*). The whole periphery of the organ forms a large striated body (*str.*) of silky fibers which are otherwise present only in the ventral organs. Near the pigmented cup, the radial fibers pass gradually into strong cords of connective tissue. The convex outer surface of the organ projected more strongly in the live animal than in the preserved specimen.

Eye organs. Each eye bears 5 organs which surround the ventral side of the eye cup in a single row. They are situated on the thin cartilage of the eye and are arranged symmetrical to the middle organ. In a longitudinal section through the row of the 5 organs, the 2 posterior organs form an exact mirror image of the 2 anterior organs; this is recognizable already by external examination (Plate II, Figure 8). The figure shows only the 3 middle organs; the sickle-shaped outer surface of the luminous bodies is situated symmetrical to the middle organ.

The middle organ of the eyes (Figure 3, *luc.oc.3*) is lens-shaped and has a strongly convex outer surface. Its luminous body is 0.9 mm wide and has a knoblike central thickening. The luminous body is bordered on the outside by a thick pad of squamous cells the refractile contents of which are shown in cross sections to be lens-shaped in the central cells and polyhedral in the peripheral cells. In contrast to the other eye organs, the central organ is surrounded by a double layer of squamous cells also on the inner side. The margin of the organ is surrounded by a ring-shaped pigmented sheath.

75 The adjacent organs 2 and 4 (Figure 3, *luc.oc.4*) differ in several respects from the middle organ. In sections their luminous body resembles a bottle that has an outwardly curved and widened neck. It is situated immediately below the outer epithelium and the terminal part of the luminous body is not covered with squamous cells; it shows the above-mentioned sickle form when examined from the outside (Plate II, Figure 8). The squamous cells form a thick cover on that part of the luminous body which does not face the middle organ and occupy the space between this part and the outer epithelium. In contrast to the middle organ, the inner surface of the luminous body is not covered with a layer of squamous cells; instead, it bears a layer of tapetum cells which is especially thick on the surface facing the middle organ. The organ is 1.3 mm and the luminous body 0.8 mm long.

The two outer organs of the eye (Figure 3, *luc. oc. 5*) are double and consist of a large peripheral and a small inner organ (*luc. inf.*). The peripheral organs, like the adjacent ones, have a bottle-shaped luminous body the long neck of which extends to the periphery and the outer surface of which is coverd by a thick pad of squamous cells. There is a tapetum, similar to that of the adjacent organs, on the inner surface of the luminous body. The organ is oval; its total length is about 1.5 mm, that of the luminous body is 0.9 mm.

The small inner organ is sharply delimited from the outer organ. It is situated below the luminous body of the large organ, nearer to its outer margin. There is a pad of squamous cells (Figure 4) between the two organs and an underlying stratum of fine fibers (*a*) with scattered nuclei of irregular form. Toward the eyeball, the inner organ is bordered by a multiple layer of small squamous cells (*c. sq. int.*) and a thick layer of pigment with spherical or oval nuclei.

Between the eye organs extend broad strands of fine connective tissue (*fibr.*) which radiate toward the periphery and converge toward the base of the organ, separating it from the underlying eye cartilage.

The **anal organs** (Figure 9) are arranged symmetrically near the rectum, slightly behind the anus. They are conical formations 1.2 mm high and 1.3 mm wide that project far into the mantle cavity. In the smaller specimen, their height and width were exactly 1 mm. The large luminous body is also conical, with the apex directed posteriorly. It is covered with a large, lens-shaped pad of squamous cells (*c. sq.*) having a strongly refractile fibrous content. There are thicker and thinner blood capillaries between these cells. The lateral surfaces of the cone bear a large pad of tapetum cells, the differentiation of which on the outer and inner surface was described above (p. 59). Between the tapetum and the luminous body is a layer of thin lamellae (*lam.*) which is thicker on the outer than on the inner surface. Thin flattened epithelium covers the inner surface of the anal organ at its boundary with the liver. On the outer side of the layer of squamous cells extends a layer of thin fibers of connective tissue which radiates
76 from the inner margin of the organ and then becomes thicker and attaches the organ to the surface of the body (*fibr.*). On the outside, i.e. toward the mantle cavity, the organ bears a thick pad of irregularly crossed cords of muscles and connective tissue which extend posteriorly to the abdominal wall. This pad is supplied by numerous, relatively thick vessels (*v.*) which pass through the tapetum into the capillary network of the luminous body. In addition, there are thick nerves (*n.*) which pass perpendicularly through the outer layer of the tapetum and extend into the luminous body, too. As noted on p. 60, those nerves which pass near the pad of squamous cells create an arcade-like pattern (Figure 14) and form a layer with numerous nuclei between the squamous cells and the luminous body.

The **branchial organs** are situated behind the base of the gills, lateral to the branchial hearts. They are more or less conical, with a rounded apex and a convex base projecting outward (Figure 17). They are surrounded on the inside by a process of the renal sac, the epithelium of which is thickened at this point. These organs are attached by strands which taper and sometimes branch, to make room for the renal sac. The branchial organ of the larger specimen (Figure 17) is 0.9 mm high and its outer surface is 1.2 mm wide. Its luminous body (*phot.*) is lens-shaped and more convex on the inner side. It is enveloped in a thin capsule of connective tissue. This capsule forms a membrane at the margin of the luminous body which separates the inner and outer fiber systems surrounding the luminous body. A thick layer of silky fibers (*s. ext.*) extends on the outside and reaches the abdominal wall. It forms a thin layer on the convex outer margin of the organ. A similar but concentrically arranged layer of fibers covers the inner surface of the luminous body (*str. int.*) and gradually extends to near the renal sac with a framework of thicker, irregularly crossed cords of connective tissue. A pad of tapetum cells situated below the luminous body is visible even in still unstained preparations, because of its yellowish color.

Ventral organs. *Thaumatolampas* has 4 ventral organs of which the 3 anterior organs are situated at about the same level as the branchial organs; the 4th organ is situated near the posterior end of the body. The 3 anterior ventral organs (Figures 15 and 18) consist of 1 small, single median organ and 2 large lateral organs. The width of the median organ is 0.6 mm, and that of the oval lateral organs is 2.3 mm. All are situated on the renal sac, the epithelium of which is also thickened around the organs. They are supplied by relatively thick vessels, 2 lateral branches of a peripheral branch of the posterior artery and 2 curved veins (Figure 15).

The middle organ has a bluntly conical luminous body, from which silky fibers radiate toward the periphery. The fibers become united on the inner side into a fibrous layer which separates the luminous body from the two cords of the musculus rectus abdominis (Figure 18). Between them and the renal sac passes the above-mentioned artery. The middle organ and the large lateral organs are covered on the outside with a thin layer of connective tissue of the abdominal wall (*m.*).

77 Closer examination shows that the large lateral ventral organs are also double. Next to the large oval luminous body there is a smaller one, closer to the wall of the renal sac and separated from the large luminous body by a thick but single layer of tapetum cells (Figure 18, *phot. ext.*, *phot. int.*). The tapetum cells, which are absent in the middle organ, divide into fibers toward the smaller luminous body (Figure 20). Silky fibers radiate from the large luminous body to the convex outer surface, forming a large, very brittle pad which causes the mother-of-pearl sheen of the organs.

The luminous body is bordered on the inner side by partly parallel and partly irregularly intertwined cords of connective tissue.

The posterior organ is the largest of all organs in *Thaumatolampas*; it is at least 3 mm wide and 0.9 mm high. Its outer surface is concave like a dish, the inner surface bears a central process which curves toward the apex of the renal sac. Surprisingly, the mantle musculature adjacent to this organ is thickened into a lens-shaped pad which fits into the dishlike concavity of the outer surface (Text Figure 20, p. 55, *luc. v.*).

The luminous body of this large organ is conical, with a flat, fused margin like a dish. Silky fibrous systems radiate from it toward the periphery (*str.*). Very large, similar fibers form a concentric pattern on the inner surface of the organ. Single groups of luminous cells may extend radially for some distance between the peripheral fibrous systems. At the center of the conical process there is a pad of yellowish tapetum cells; unlike the tapetum cells in the lateral ventral organs, these cells do not form a separate, smaller luminous body.

Measurements of the two specimens of *Thaumatolampas diadema*

	Specimen from Station 89	Specimen from Station 118
Total length to apex of 4th arms	48 mm	43 mm
Dorsal length of mantle	30 mm	21.5 mm
Maximum width of mantle	12 mm	10.5 mm
Width of head	13 mm	11.5 mm
Dorsal base of fin	14 mm	11 mm
Width of a fin	14 mm	11 mm
Length of the 1st arm	12 mm	10 mm
Length of the 2nd arm	14.5 mm	12.5 mm
Length of the 3rd arm	12.5 mm	10.5 mm
Length of the 4th arm	13 mm	10 mm
Length of tentacle	20 mm	

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2. Subfamily: *Enoploteuthinae* CHUN

Tribe I: Enoplomorphae CHUN

Abraliopsis JOUBIN, 1896

Abraliopsis morisii VERANY
(Plates V–X)

Onychoteuthis morisii VÉRANY, 1837, p. 2, Plate II a.
Abralia morisii GRAY, 1849, p. 50.
Enoploteuthis hoylei PFEFFER, 1884, p. 17, Plate III, Figures 22, 22 a, 22 b.
Abralia morisii HOYLE, 1886, p. 38.
Abraliopsis pfefferi JOUBIN, 1896, pp. 19–35, Figures 1–10.
Abraliopsis hoylei JOUBIN, 1896, p. 33.
Abralia lineata GOODRICH, 1896, p. 10, Plate III, Figures 46–50.
Abraliopsis morisi PFEFFER, 1900, p. 168.
Abraliopsis hoylei HOYLE, 1904, pp. 36, 58–64, Plate I, Figure 3, Plates VIII, X.

JUVENILE FORMS
Teleoteuthis caribbaea JATTA, 1896, pp. 100–102, Plate XIII, Figures 35–41.
Micrabralia lineata PFEFFER, 1900, p. 167.
Compsoteuthis lönnbergi PFEFFER, 1900, p. 167.
Abraliopsis juv. ISSEL, 1908, p. 210, Plate IX, Figures 15–21.

Localities: Station 54: Guinea Current, 1°51′ N, 0°31′ E. Vertical net to 2,000 m—One male with hectocotylus.
Station 254: Indian North Equatorial Current, 0°29′ S, 42°47′ E. Trawl, 977 m—male.
Station 256: Indian North Equatorial Current, 1°49′ N, 45°29′ E. Trawl, 1,134 m—mature female.
Station 265: Indian North Equatorial Current, 6°24′ N, 49°31′ E. Trawl, 628 m—Stomach contents of *Coloconger raniceps* ALCOCK.

Older juvenile forms were caught in the Guinea Current (Station 54) and in the Indian Countercurrent (Stations 223, 228, 231).

Abrialiopsis morisii has been described more or less in detail by early and recent authors. As happens so often in such cases, the older descriptions suffer from such inaccuracies that they left later observers uncertain whether their specimens actually belonged to the previously described species. It is therefore necessary to review the synonymy and, furthermore, to consider also the closest
79 relatives of this species. This is the more desirable as PFEFFER, in his recent study "Die Gattungen *Abralia*, *Abraliopsis* und *Asteroteuthis*" ["The genera *Abralia*, *Abraliopsis* and *Asteroteuthis*"] (1908, p. 289ff.), has already made a clever attempt at clarifying the existing confusion.

Pfeffer distinguishes between two groups of forms, which he names the *veranyi* group and the *hoylei* group. To facilitate the understanding of the following discussion, it may be mentioned that in my systematic review of the Enoploteuthidae (p. 48), I defined the *veranyi* group as the genus *Abralia* and the *hoylei* group as the genus *Abraliopsis*; referring to diagnoses given in that review, I would emphasize that Pfeffer correctly placed *Enoploteuthis owenii* Vérany in the *veranyi* group (*Abralia*). On the other hand he attempts to prove that *Onychoteuthis armata*, described by Quoy and Gaimard (1833, Vol. II, p. 84; Plate 5, Figures 14–22), and Vérany's *Onychoteuthis morisii* belong to the *hoylei* group (*Abraliopsis*).

I agree with Pfeffer only as regards *Onychoteuthis morisii* but not as regards *Onychoteuthis armata*. As the latter species is of particular importance for our systematic discussion—because it is the one described earliest—we shall outline the reasons which induced Pfeffer to place it in the *hoylei* group. Pfeffer considers the arrangement of luminous organs and the coloration of the buccal funnel to be the decisive characters.

d'Orbigny (1835–48, p. 340, *Onychoteuthis*, Plate 14, Figures 11–15) corrected the incomplete description of Quoy and Gaimard after having examined the original specimen. Pfeffer, however, notes that the measurements of Quoy and Gaimard do not agree with those given by d'Orbigny and assumed, therefore, that d'Orbigny had examined a different specimen. This controversy can of course no longer be settled, but I assume that d'Orbigny did in fact examine Quoy and Gaimard's original specimen and that the measurements given by them were inaccurate.

To judge from Figure 11 on Plate XIV of d'Orbigny, the position of the luminous organs on the ventral side of the mantle agrees well with the conditions observed in *Abralia* but differs markedly from those in *Abraliopsis*. After a thorough comparison of specimens of *Abralia* from Nice with the above figure, I find that the luminous organs are indeed sometimes arranged in transverse rows, but they may also cross each other in obliquely diagonal rows, resembling those shown by d'Orbigny. Pfeffer does not accord this point any consideration but stresses that the biserial arrangement of luminous organs on the ventral surface of the 4th arms shown in the figure speaks against the inclusion of *Onychoteuthis armata* in the *veranyi* group. I would like to make the following comment on this point.

d'Orbigny illustrated only the base of the 4th arms. In *Abralia* and *Abraliopsis*, this part of the arms has luminous organs in 3 rows. It is only further distally that the dorsal row bifurcates in *Abralia*, so that the quadriserial arrangement of light organs is obtained that is characteristic for this genus. d'Orbigny apparently paid only cursory attention to this basal part of the arms, as otherwise he would have shown also the luminous organs situated in both genera on the margin of the tentacle (Plate V, Figure 2). I am therefore of the opinion that d'Orbigny's description of the luminous organs at the base of the arms is too superficial and does not present the conditions in the two genera
80 accurately. His drawing of the luminous organs on the surface of the mantle, on the other hand, is indeed characteristic for the *veranyi* group (*Abraliopsis*).

Pfeffer writes further that "the position of *O. armata* in the *hoylei* group is determined by a character not mentioned in the description of d'Orbigny but clearly shown in his drawings, i.e. the violet coloration of the buccal membrane with its violet-white pillars and points". In the copy of the monograph at my disposal (from the library of Leipzig University), the buccal funnel is not shown violet. It has the same light flesh-red color as the arms, and wine-red buccal pillars. The illustration thus again suggests the *veranyi* group (*Abralia*) and not the *hoylei* group, in which the buccal funnel is strikingly dark violet.

Contrary to Pfeffer, I conclude therefore that *Onychoteuthis armata* is an *Abralia* and belongs

to the *veranyi* group of Pfeffer. This conforms also to d'Orbigny's important statement that the tentacle club of the specimen bears "quatre crochets avec une ligne de cupules", which is a condition that is correct for *Abralia* but not for *Abraliopsis*.

I carefully examined the clubs of the three specimens of *Abralia* (all mature females) and found in two specimens 4 hooks in a row, the 3rd specimen had only 3 hooks on each tentacle. Pfeffer noted 4 hooks and stated correctly that on the proximal hand part the ventral longitudinal row was absent and that the mediodorsal and dorsal rows each consisted of 4 suckers. In my specimen with 3 hooks, the mediodorsal and dorsal longitudinal rows also consists of only 3 suckers each. The hand part of all specimens bears distally the usual 4 suckers which rapidly decrease in size.

As already mentioned, I fully agree with Pfeffer that *Onychoteuthis morisii* (Vérany, 1837) belongs to *Abraliopsis*, to i.e. the *hoylei* group. This is evident not only from the illustration but, especially, from the description of the coloration of the 8-radiate buccal funnel: "d'une couleur brune noirâtre à angles blanchâtres".

Gray (1849) established his genus *Abralia* for two species; this genus was divided by Joubin (1869) into the two genera *Abralia* (*veranyi* group) and *Abraliopsis* (*hoylei* group). I therefore disagree with Pfeffer who assigned two generic names to the *hoylei* group but none to the *veranyi* group. The name *Asteroteuthis* proposed by Pfeffer for the *veranyi* group is unnecessary and we have to follow Joubin with whom Pfeffer previously agreed (1900).

Joubin has undertaken a detailed comparison of his Mediterranean specimen of *Abraliopsis morisii* with a specimen of *Enoploteuthis hoylei* sent to him by Pfeffer and attempts to prove that they belong to two different species. Examination however shows that the differences he presents comprise relative characters which are well within the range of variation of this cosmopolitan form. The procedure of Joubin calls for care in the evaluation of relative characters for the systematic definition of species of
81 Cephalopoda. In any case we have for *Abraliopsis morisii* a much more detailed description than of any other known species of the Enoploteuthidae; Goodrich (1896) furnished a description—under the name *Abralia lineata*—of a specimen caught in the Bay of Bengal; Hoyle (1904), moreover, complemented Joubin's description in several points and also described the characters of the male.

In view of the above mentioned studies by so many authors, a new description of this species seems unnecessary, at least for the external characters. However, I believe I can add in some respects to the previous descriptions and also clarify the postembryonic development of the species almost completely. The genital conditions, moreover, also show a number of special characters worth mentioning.

External characters

The **shape of** the **body** of *Abraliopsis morisii* is mainly characterized by the fins, which form a broad arrowhead. The curved anterior base of the fins projects far beyond their dorsal attachment and their length is about $\frac{3}{4}$ of the mantle length. The fins taper sharply toward the pointed posterior end of the body. As will be shown below, their relative size varies markedly during postembryonic development, and the posterior end of the mantle may be blunt or slender-conical, depending on the age of the animal.

The head bears a number of **folds**, which have not been described by any other observer. Only Pfeffer mentions in his general description of the Enoploteuthidae that transverse and longitudinal neck folds are often well developed.

In the largest specimen at my disposal, a mature female, the neck bears a dorsal median ridge which

extends to the neck cartilage. This is less distinct in younger specimens. The median ridge is flanked on each side by a large, oblique, crescent-shaped neck fold, which is followed laterally and ventrally by 3 pairs of small neck folds. They originate from a transverse ridge which forms the boundary between head and neck. The first or dorsal neck fold passes obliquely toward the neck fold. In the large, mature specimen (Plate V, Figure 1), the two folds unite into a long lamella which is narrower in the middle. In younger specimens, the two folds are separate or connected by a very thin ridge. The second or middle neck fold bears the oval, laterally compressed olfactory tubercle. The ventral folds are situated on each side near the funnel and form tubercles.

The **arms** do not differ much in length, but the ventral arms are longer than the others. The formula is 4, 2, 3, 1, i.e. as recorded by Hoyle, although in his specimen it applies only to the left side while for the right side of his specimen it is 2, 3, 1, 4.

82 All arms have swimming membranes. On the 1st and 2nd arms, they form weakly developed keels only in the distal half. The swimming membranes of the 3rd and 4th arms are well developed and extend to the base. The swimming membrane of the 4th arm is displaced slightly dorsally and extends at its base to the 3rd arms without passing directly into the membrane of the 3rd arm.

The protective membranes, which Hoyle simply designates "muscular lobes with thin, membranous connecting membranes", are on all arms broader on the ventral than on the dorsal side. This is especially the case on the 3rd arms; the protective membranes are weakly developed on the 4th arms, except in the mature male.

All arms bear two alternating rows of hooks which develop by transformation of suckers during postembryonic development. It is therefore not surprising that even the arms of the largest specimens still bear a few pairs of very small suckers that have not been transformed into hooks. For example, the largest female in our collection bears 10, 10, 12 and 11 pairs of hooks on the 1st, 2nd, 3rd and 4th arms, respectively, and 5, 2, 5 and 2 pairs of very small apical suckers.

We caught a beautiful male specimen with a large, orange protective membrane on the left ventral arm. This specimen is shown in Plate VI, Figure 1, prepared after watercolor sketches made to reflect the colors as accurately as possible; the **hectocotylized left ventral arm** is shown in Plate X, Figure 1. Hectocotylization of the left ventral arm was first observed by Hoyle; Pfeffer (1894, p. 18) and Jatta (1896, p. 102) had earlier interpreted the 3 dark-pigmented terminal knobs of the ventral arms of both sexes as characters of hectocotylization.

Males apparently are caught more frequently than females. Our expedition collected 2 males and one mature female; in the material of the German South Polar Expedition, I found 3 males but no females. I examined the genitalia of all specimens and was thus able to determine the beginning of hectocotylization more accurately.

The hectocotylized left ventral arm has a large ventral protective membrane which is traversed by long muscular supports. The latter are surrounded by small papillae which are also present on the ventral protective membranes of the other arms. All bases of the arms of males also bear conical processes which usually become smaller distally and do not connect with the muscular supports of the protective membrane that follow. The number of these processes usually increases from the dorsal to the ventral arms; on the hectocotylized arm they are numerous and densely arranged.
83 Another character of the hectocotylus is that the hooks in the ventral row are smaller than in the dorsal row. The hectocotylized arm shown in Plate X bears 31 hooks and a single small distal hook, i.e. 16 pairs. This corresponds to the 16 muscular supports on the protective membrane.

The largest number of hooks, which I found on the hectocotylus of an adult male, was 18 pairs.

These characters of the hectocotylus, some of which were described by Hoyle, apparently develop only shortly before sexual maturity. That the two specimens which are of the same size as the male shown in Plate VI were males too, was determinable only by dissection. The left ventral arm of these specimens showed no trace of a transformation, and I therefore had assumed that they were females. The only indication of a secondary male sexual character in these specimens was the presence of several conical papillae on the bases of the arms. In one of these young males I found small whitish warts which covered the base, the muscular bridges and the gaps between the hooks on the inner surface of the dorsal arms. The left ventral arm of this specimen had 9 pairs of hooks which were not larger in the dorsal row, nor were they covered by a widened protective membrane. This relatively late and apparently rapid development of the hectocotylus is particularly interesting because in *Pterygioteuthis* the transformation of one of the ventral arms into a hectocotylus begins very early.

The **tentacle** has an only slightly widened club, as already noted by Joubin. The club is divided into a proximal carpal part and a distal hand part. The **carpal part** usually consists of 5 suckers, between which are situated 5 adhesive knobs. In some cases, the adhesive knobs are more numerous and only indistinctly developed. The explanation for this may be that the suckers do not always adhere to the opposite tentacle at precisely the same point. However, I also found clubs with only 3 suckers, as on the right club of the mature male shown in Plate VIII, Figure 4, which differs from the left club of this specimen—that has 5 carpal suckers—also by a larger number of hooks.

The **hand part** of the club also shows numerous variations. It is sharply separated into a proximal half, covered with hooks, and a distal half with quadriserial rows of suckers. According to Joubin (1896) and Pfeffer (1908, p. 289), both lateral rows in the proximal half of the hand part are suppressed and only hooks in a biserial arrangement are present. Closer examination, however, reveals that the hooks always alternate with the dorsal marginal suckers (Plate VIII, Figures 3, 4). In the male the club of which is illustrated in Figure 5, all suckers except one were apparently lost, since their insertions are still visible. Hoyle (1904, Plate VIII, Figure 1) illustrates a similar club with one persisting dorsal sucker. The dorsal hooks are always smaller than the ventral hooks, as Pfeffer stated. All hooks are surrounded by the soft part of the original suckers, which often extends like a mantle or sheath to the apex of the hook.

84 The **number of hooks** varies widely. Pfeffer states in his diagnosis of the *hoylei* group that these species have 4 large ventral and 4 small dorsal hooks. None of my specimens shows such a condition; Hoyle also found only 3 ventral hooks in his specimens. The club of the mature female (Plate VIII, Figure 3) had 3 large ventral and 3 small dorsal hooks, and so had the male with hectocotylus (Figure 5). An idea of the variation of the number of hooks can be obtained from the club of the largest male (Figure 4), which bears 7 hooks (4 ventral and 3 dorsal ones) on the right tentacle and 5 hooks on the left. The tip of the club is usually somewhat curved dorsally and always has a distinct dorsal keel (swimming membrane) (Figure 3).

The protective membranes are very narrow in the proximal part of the hand, but the ventral protective membrane is widened like a comb from the carpal part to the first hook, and then abruptly flattens (Figure 3). The club of males were characterized by particularly weakly developed membranes.

Earlier authors failed to supply detailed information on the **buccal funnel** and the **attachment of the arms** (Plate VIII, Figure 1). They agree, however, that the buccal funnel has 8 points, as noted already by Vérany (1837). The 8 spindle-shaped buccal pillars, which support the funnel, end in 8 points at the margin; the strong central nerve is visible indistinctly through the pillars. As in *Thaumatolampas*, the base of the 3rd pillar bears knoblike swellings which are situated on the dorsal wall of the pillar. Contraction of the dark violet buccal membrane which connects the pillars closes the

buccal funnel, as shown of the male in Plate X, Figure 1. The buccal membrane is smooth on the outside; its inner side, however, bears small villi that extend to the buccal cone; the latter has a thin outer lip with a sharp edge and a higher, fluted inner lip.

The **attachments**, which extend from the pillars, are typical for the Enoploteuthidae (p. 15) in that the 4th arms have dorsal attachments. The membranes of attachment extend on all arms for a short distance along the base without passing directly into the adjacent protective membrane.

The arms are connected by thick, muscular attachments of two types: superficial ones and deep ones. The superficial attachments are conical muscles which extend from the ventral side of the base of the arm to the next arm (Plate VIII, Figure 1, *fun.br.*^{2}). They extend symmetrically—from the left side of the base of the arm on the left half of the body, and from the right side on the right half.

The attachments which extend from the 3rd to the 4th arms meet in the middle and form a kind of chiasma (Plate X, Figure 1).

The deep attachments which extend from the 3rd to the 4th arms meet in the middle and form a kind of chiasma (Plate X, Figure 1).

The deep attachments consist of conical cords of muscles which pass in the direction opposite to that of the superficial attachments, i.e. from the dorsal side of the base of the arm to the ventral side of the preceding arm (Figure 1, *fun.br.*^{3}). Both types of attachments enable the arms to be tightly folded together when they are curved inward.

85 The tentacles, too, are attached by a slender muscle; it descends deeply behind the chiasma between the 3rd and 4th arms (*fun. tent.*).

The buccal funnel is thus situated on the bases of the arms and is connected to them by the attachments from the respective pillars. The base of the buccal funnel is deeply invaginated and finally becomes fused with the pharynx. Between the attachments on the bases of the arms and the outer wall of the buccal funnel are pocket-like spaces the slitlike openings of which are named, correctly or not, "pori aquiferi". *Abraliopsis* has 6 such pores which are the openings of 3 pairs of lateral pockets between the attachments. The dorsal pocket is so small that it hardly has a separate pore, while the opening of the ventral pocket is covered by a thin lamella.

The knobs on the 4th arms

The 3 dark terminal knobs on the 4th arms are a special character of the genus *Abraliopsis*; their construction, therefore, is of special interest. Joubin (1896) examined sections of these swellings, but owing to the poor condition of his material his data are so vague that a description after a well-preserved specimen is desirable.

The knobs are of about the same size, but the middle knob is sometimes slightly larger. Sections (Plate VIII, Figure 7) show that their blackish coloration is caused by large, dense chromatophores with a dark content which surround the knobs. Joubin's illustration of a cross section of the tip of the arm shows that the knobs are embedded eccentrically in the cutis. They are hemispherical in cross section, rarely more or less kidney-shaped. In addition to the pigmented envelope, the knobs are surrounded by thin strands of connective tissue which also form a kind of envelope. The interior of the knob consists mainly of loosely arranged cells which are polyhedral or tubular and may have ameboid processes (Figure 8). The nuclei of these cells are spherical, rarely oval; they usually have a single nucleolus. The cell content consists of light-colored granules which would be considered as secretory granules in gland cells. These granules fill the whole cell uniformly and stain dark blue with iron-

hematoxylin. Only once did I find a central band of cells which widened like a funnel toward the periphery. These cells gave the impression that they had gelatinously degenerated; their outlines were indistinct or only indicated by vacuolated places. The normal cells are loosely arranged with a dense, well-developed capillary network in the gaps between them (Figure 9). The nuclei of the capillaries are generally smaller; they stain more intensively and often appear as dark lines, because they are flattened. The capillaries enter the cells in many places, which is most conspicuous at points where
86 the small vessels are cross-sectioned at a right angle. The finest capillaries sometimes show a delicate, transverse striation which is caused by groovelike muscle fibrils. The capillaries usually extend from the side which faces the arm musculature; they often extend a considerable distance through the network of the tissue.

Joubin's description (p. 27) suggests that his material must have suffered from maceration, as he describes 4 categories of cells, in addition to a network of connective tissue and a hyaline cartilage in the content of the knob. I found no such elements in my material, which was preserved in formol.

I must admit that I have no explanation for the function of these knobs. The granulate content of the cells resembles that of glands, but no lumen of a duct or opening could be found. The unusually thick pigmented envelope excludes their serving as phosphorescent knobs.

It is of little use to speculate on the function of formations which cannot be observed in live material because of the rarety of material.

The **coloration** of the adult animal is vivid. Its pink or reddish-brown background color is caused by the numerous chromatophores on the mantle, the free parts of the funnel, the head and the outer surface of the organs. Brownish-yellow chromatophores are concentrated at the side of the gladius and produce the orange-brown tone of the mid-dorsal line. Particularly prominent in younger specimens and in males are two large chromatophores on the sides of the posterior end of the liver (Plate VI). As already stated by Vérany, the buccal funnel of all specimens has a dark-violet color, which is apparently characteristic for the species.

Luminous organs

The rich coloration and pattern on the body of these animals is markedly intensified by numerous luminous organs which I have earlier described in detail (1903). Without knowledge of my data, Hoyle (1904, pp. 59–64), once more described them thoroughly, a year later. Comparison of his drawings with mine shows that our descriptions differ little.

As regards the arrangement of the luminous organs, all observers are agreed that they form rows on the mantle, head and ventral arms. This is particularly distinct on the mantle in younger specimens and in males, in which each side of the ventral surface bears 3 rows from the posterior end of the body to the margin of the mantle and the outer row is directed toward the ventral corners of the mantle. As new organs are constantly being formed between the older organs, the pattern of rows becomes
87 indistinct in larger specimens. There are scattered organs also on the dorsal surface and the lateral parts of the mantle; in young specimens, they form a longitudinal row on each side. The funnel, too, has 4 stripes of organs on its outer surface; they are a continuation of the two middle rows on the mantle.

The head bears a single median row which is formed by confluence of two branches near the funnel margin; this row divides at the base of the ventral arms and continues on the ventral side of each ventral arm. This single cephalic row is flanked by two inner rows which extend on the dorsal

margin of the ventral arms to the tips. There are also two outer rows on the head which begin at about the level of the olfactory tubercle, pass over the eyeball and continue ventrally from the high swimming membrane on the 3rd arms to the tips. In the larger females, these rows have short branches toward the dorsal margin of the 4th arms. A circle of organs surrounds the eyelid. Fins, tentacles and both dorsal pairs of arms bear no luminous organs.

Joubin, Pfeffer and others failed to notice a number of slightly larger organs that are present on the ventral side of the eyeball in addition to the small and scattered organs described above. The ventral inner surface of the eyeball bears a row of 5 organs, of which the two outer ones are larger. Hoyle, too, noted these organs, the strong sheen of which is striking in live animals (Plates V, VI).

Detailed structure of the luminous organs

(Plate X, Figures 6, 7)

1. Skin Organs

The skin organs are of a complicated structure. A lens is situated in front of the luminous body; there is also a large reflector which is surrounded by a pigmented envelope; around these formations, furthermore, there are differentiations which apparently are characteristic for *Abraliopsis* and the related genera *Abralia* and *Enoploteuthis*.

The **luminous body** (internal cone of Hoyle) is situated in the center of the organ, surrounded by the lateral walls of the reflector and bordered anteriorly by the posterior margin of the lens. It consists of two parts, of which the posterior is a pointed cone, while the anterior part is wide and flattened (Figure 7, *c. phot.*). The two parts differ in structure: the nuclei of the posterior part are large, spherical or oval, less often of irregular form, and embedded in a pale mass without distinct cell boundaries;
88 the anterior part is strongly refractile because of the presence of numerous spherical or, occasionally, irregularly formed shining flakes between which the nuclei become compressed into irregular, often crenate forms. This layer apparently corresponds to the strongly refractile spherical bodies observed by Joubin (1895) in the center of the luminous organ of *Abralia*. In an *Abralia* caught in the Indian Ocean (Station 249) which unfortunately was severely damaged, I found that these flakes consist of two unequal, crescent-shaped halves which are crossed at a right angle. In *Enoploteuthis leptura*, too, I found a spherical, striated formation in the center of the luminous body; neither in this body, nor in the analogous formations in *Abralia* were any nuclei detectable.

Hoyle does not mention a division of the luminous body into two parts but stresses the irregular form of the nuclei.

The **reflector** surrounds the luminous body; it consists of two separate parts (Figure 7, *refl.'*, *refl."*). The hemispherical inner part consists of concentric layers and is situated on a thick, funnel-shaped part which surrounds the luminous body on both sides and widens toward the outside. Hoyle names the unpaired hemispherical posterior part of the reflector "posterior hemisphere" and the lateral part "inner cup". The inner cup also consists of concentric lamellae, between which occasionally are elongate nuclei.

A large lens (*l.*) lies in front of the refractile part of the luminous body which appears in sections as a rectangle with convex outer surface. The lens consists of fine, fibrous tissue the thicker fibers of which surround spindle-shaped elements that cannot be considered as cells because the nuclei are usually situated between them. The thin fibers of the lens stain intensively bluish with iron-hematoxylin.

Around the organ, especially on its posterior side, are large lacunae (*lac.*) which are traversed by

septa of connective tissue. On the outer side, i.e. near the lens and the anterior margin of the reflector, we find a framework of thicker fibers of connective tissue (*f.*) with oval nuclei. This framework is pervaded by capillaries and passes at the outer margin of the lens into thinner fibers (*fibr.*).

The connective tissue of the cutis around the organ is slightly denser in the vicinity of the lacunae, forming an external envelope.

The **pigmented sheath** of the organs consists of a number of chromatophores which are situated not in the area of the lacunae but close to the reflector. A large central chromatophore covers the hemispherical posterior part of the reflector; its lateral walls are surrounded by several chromatophores which apparently form two rows. These chromatophores sometimes extend to within half the height of the lateral margin of the lens; but they do not constrict the lens, as described by Hoyle. Between the chromatophores and the reflector are numerous oval nuclei embedded in a finely granulate cytoplasm. I could not find nerves to the luminous body; however, such nerves may be present.

89

2. Eye Organs
(Plate X, Figure 6)

In my first communication (1903), I already reported that *Abraliopsis* is characterized by a marked dimorphism of structure of the luminous organs. The eye organs differ markedly in structure from those of the skin—only the luminous body is similar. The eye organs are flat and lens-shaped; the terminal organs are larger, nearly 0.3 mm wide. The eye organs have no reflector, pigmented sheath or lacunae. They are situated partly on the eye cartilage and partly on the layers of connective tissue of the eyeball.

The luminous body is flattened like a cake and has, again, numerous spherical, oval or irregularly crenate nuclei. As in the skin organs, it contains a strongly refractile central mass, but without nuclei. We may assume, however, that this formation is homologous with the anterior part of the luminous body of the skin organs. The entire luminous body is surrounded on the outside by a beautiful radial circle of long fibers, some of which are bent or curved at the margin. Closer examination shows that these fibers are elongate cells with a very long, slender central nucleus. The organ is covered with a thin layer of cutis that has numerous nuclei and that extends to the site between the fibers and the eye cartilage. I found no nerves in this cutis, although a number of fibrous cords can be traced from the outer layer of the retina to the region of the luminous organs. Hoyle gave a generally correct description of these formations. But he interprets the homogeneous refractile substance in the luminous body as a lens. The central position of the refractile substance, however, rules this out.

Eye Organs of *Abralia*

Luminous organs on the eyes are also present in *Abralia* but have been overlooked by all other observers. The eye of *Abralia* bears 5 organs which are situated on each side of the ventral surface of the eyeball. The 3 middle organs have the same nacreous sheen as those of *Abraliopsis*. The central organ is only slightly larger than the two adjacent organs; in the largest specimen it was 1.2 mm wide, in the adjacent organs, 0.9 mm. The two marginal organs are much larger—about 4 times as large as the middle organ. They are oval and 4 mm long in a mature female. It is surprising that these large organs were overlooked by earlier observers. In contrast to the smaller organs, the large ones lack the nacreous sheen and, instead, have a whitish color.

90 I examined sections of these organs but must point out that they were not sufficiently well preserved to reveal their finer details. A few structures, however, were recognizable. The eye organs are dimorphic. The 3 middle organs resemble those of *Abraliopsis*: they have no pigmented sheath and their surface is covered with a pad of fine radial fibers. Below this is the luminous body with rounded nuclei and spherical refractile flakes. In contrast to the organs of *Abraliopsis*, a reflector occurs near the eyeball; it consists of short, undulate lamellae, similar to those which cause the metallic sheen of the skin of various Cephalopoda. Squamous cells are not recognizable in the reflector, but there are irregularly distributed small, spherical or oval nuclei.

The large marginal organs have an entirely different structure. Their luminous body is not covered by a circle of radial fibers; however, it is very large and forms the greater part of the large organ. The luminous body is covered by cutis at the periphery and bordered toward the eyeball by a large reflector which resembles in structure that of the small organs. The reflector widens slightly at the margin and fuses with that of the small organs.

The luminous body, unfortunately, yielded only incomplete information. Radially arranged strands of cytoplasm were recognizable, with small, spherical nuclei and numerous small, strongly refractile granules. At some sites there are also larger refractile flakes, resembling those in the luminous body of the small organs. Refractile granules are absent in the basal part of the luminous body, which borders on the reflector. The arrangement of the whole mass of the luminous body in radial strands is apparently caused by the vessels between the radial strands. Unfortunately, I am unable to give a satisfactory explanation about this arrangement.

All the above reported indications are at least sufficient to conclude that the Mediterranean *Abralia* has 3 different types of luminous organs: skin organs and large and small eye organs.

Mantle complex

(Plate IX)

Opening of the mantle cavity from the ventral side shows that a thin median septum connects the mantle with the visceral sac and passes into the very thin abdominal wall, which was flesh-pink in a male (Plate IX, Figure 2). This pigmentation extends to the base of the gills; it is slightly more vivid near the spermatophore sac.

The funnel has a somewhat curved posterior margin. Its posterior half is not pigmented and
91 has no luminous organs. The funnel cartilages are of simple form, straight, and only rarely a little widened at the posterior margin. A deep groove, which is shallower anteriorly and posteriorly, extends along the funnel cartilage and accommodates the elongate mantle cartilage; the latter is longer than the funnel cartilage and extends toward the ventral corners of the mantle. In the largest specimen the funnel cartilage is 5 mm long and 1.7 mm wide. The funnel depressors extend as thick cords into the posterior dorsal wall of the funnel, taper toward the base of the gills and end in a point (Figure 4).

The rectum, visible between the funnel depressors in the anterior part of the mantle complex is conspicuous by its dark-violet or brownish pigmentation. This becomes weaker toward the anus, which is bordered by two lips and has two lateral symmetrical anal papillae of spatulate form. On the right side of anus and rectum passes the vena cava, which forms an S-shaped loop in front of the renal sac and then passes into a large median venous sac and into lateral sacs which extend to the branchial hearts. The lateral sacs receive posteriorly the two abdominal veins which open at a point

closer to the midline than it is in other Oegopsida. The branchial hearts are not widely separated; their appendages are small, knoblike and clearly visible on their posterior surface.

The gills extend to the posterior margin of the funnel; a ligament median to the mantle cartilage attaches them to the mantle. In the large females, each gill bears 20 alternating lamellae on both sides. The inner lamellae, situated near the mantle, are more loosely arranged than the outer or ventral lamellae. The latter are not much shorter than the inner lamellae. The branchial vein passes over the ventral comb of the gill; it gradually widens toward the base and then descends deeply behind the renal sac.

The posterior artery is relatively short and the pallial artery, which passes along the anterior margin of the mantle septum, branches from it. The posterior artery divides into two branches, the lateral posterior arteries (*a.pinn.*), which surround the visceral sac and supply blood mainly to the fins.

If the renal sac is not filled with whitish detritus, its two outer openings are distinct as oval, slightly raised papillae.

Genitalia

Except for one mature female, my material consists only of males. As the development of the hectocotylus apparently takes place after the maturation of the genital products, the sex of smaller specimens can only be determined by dissection.

92 **Male genitalia**. The conical testis extends to near the posterior end of the body (*test.*). A gonoduct is developed only on the left side; it covers the intestinal tract together with the testis. The gonoduct opens in a spermatophore sac (*pen.*) which is situated behind the base of the left gill and projects markedly into the mantle cavity. The spermatophore sac of one specimen was a vivid rust-red in the middle. The appendage of the prostate (Figure 1, *app. prost.*) projects into the mantle cavity directly from the base of the gills. A part of the spermatophore sac and the 2nd and 3rd part of the seminal vesicle are also visible in the anterior part of the mantle cavity. If the male gonoduct is laid free by dissection (Plate IX, Figure 5; Plate X, Figures 2, 3), the vas deferens becomes visible which opens in the body cavity by a funnel-shaped opening behind the seminal vesicle. The vas deferens passes in undulate curves on the dorsal surface of the spermatophore gland and then opens in its anterior part. As I noted previously (1905, p. 644), the seminal vesicle—or spermatophore gland according to Marchand (1907)—of the more primitive Oegopsida is distinctly divided into 3 parts. In *Abraliopsis*, the first part is slightly larger than the second part; it is more or less rectangular and has ventral lobes, through which the gland ducts are visible (*ves. sem.'*).

The second part is distinctly folded and shows a number of gland ducts which are arranged like a fan (Plate X, Figure 2). The slightly *S*-shaped duct for the developing spermatophores is visible on its ventral posterior surface.

The third part has smooth walls and is very long. Its wider proximal half surrounds the posterior side of the second part and narrows distinctly where it reaches the distal half, which is curved anteriorly. This narrows suddenly before it opens into the accessory gland, which was previously named prostate (*prost.*). The accessory gland forms a long tube which is curved posteriorly and is situated on the spermatophore gland. The accessory gland bears longitudinal swellings; at its junction with the terminal part of the spermatophore gland it bears a caecum, which was named appendage of the prostate (*app. prost.*) in the past. As Marchand showed, this appendage is the initial part of the vas

efferens (*v. eff.*), which is curved in a loop and consists of two closely situated branches. The vas efferens has thus two lumina which unite at the apex of the appendage. One of the lumina leads directly into the vas efferens, the other into the prostate. The vas efferens ("distal vas deferens" of Marchand) is short and opens in the posterior third of the spermatophore sac (*b. sperm.*), which is slightly curved toward the other parts of the duct apparatus and is slightly spirally coiled where it opens to the outside at the base of the left gill.

93 The spermatophore sac was filled with spermatophores in 2 males. The spermatophores form a slight spiral in the sac, corresponding to the coiling of the sac; the aboral pole of the spermatophore (i.e. the pole containing the sperm) is always directed toward the opening of the sac. The spermatophores glide in the same position through the caecum and the vas efferens and then pass successively into the spermatophore pocket. However, they are orientated in the opposite direction in the seminal vesicle (spermatophore gland), particularly in its 3rd part. A reversal during the advance of the spermatophore can only take place at a point like the head of a railroad roundhouse. I assumed previously that the caecum of the prostate serves as this turning point. However, it later became clear that the caecum contains two ducts which become united. This makes it unsuitable as a turning point, but we agree with Marchand, who considers the prostate as the turning point. The spermatophores are pushed in with the aboral end forward when they leave the 3rd part of the seminal vesicle. As they are now situated in a caecum with a single lumen, the spermatophores can leave it only with the pointed end forward. They pass in this position through the winding initial part of the vas efferens (caecum of prostate) and finally reach the spermatophore pocket.

A duct which I named "ciliated duct" extends from the terminal part of the spermatophore gland along the entire posterior margin of the prostate and finally opens in a ciliated funnel. In a previous description (1905), I attempted to prove that the ciliated duct is homologous with the duct described by Brock (1879, p. 19) in the same position in *Sepia*. However, Brock did not notice that this duct opens via a funnel into a pocket which he and Grobben (1884, p. 14) named "peritoneal pocket". According to Brock, the peritoneal pocket is completely closed; Grobben considers it as a secondary part of the body cavity, constricted from the capsule of the testis. I proved, however, that this pocket is not part of the body cavity but a pocket which opens freely into the body cavity near the branchial heart. This "genital pocket" is not related genetically to the body cavity; it is a caecum which is lined with ectoderm and opens to the outside (p. 29). The margins of the genital pocket are usually fused with the terminal part of the spermatophore sac so that it forms a completely closed space.

As to the morphological value of the ciliated canal, it is important that the ciliated funnel opens not in the body cavity but to the outside, i.e. into a genital pocket formed by an invagination of the outer surface of the body.

Female Gonoducts
(Plate IX, Figures 3, 4)

I had only one female of *Abraliopsis*. The mantle complex of this mature specimen is shown in
94 Figure 3. Surprisingly, nidamental glands are absent. The female has instead unusually well-developed oviduct glands which are remarkable by their swollen condition and their position. The oviduct glands are situated near the midline of the body and are closely contiguous, covering the rectum and vena cava completely. These glands resemble the halves of a coffee bean, and look like a single entity. Lateral examination shows, however, that this is not the case (Figure 4). The gaping dorsal and ventral

halves are connected and are the swollen openings of an oviduct filled with ripe eggs 1 mm long. The regular, comb-like arranged lamellae of the oviduct glands, the outline of which forms concentric stripes on the outer surface, are visible on the contiguous surfaces.

The wedge-shaped glandular pads which are united over the base of the gills on each side are the oviduct glands, which are situated in the dorsal and ventral lips of the opening of the oviduct. The eggs are covered directly during oviposition with the mucous secretion of the oviduct gland without a secretion of the nidamental glands.

As I had only one female of *Abraliopsis*, I examined the closely related *Abralia* to obtain information on the peculiar displacement of the openings of the oviducts toward the middle of the body. Some young specimens of *Abralia veranyi* Rüpp. of both sexes from Nice gave the desired information. Figure 6 shows that the oviduct of the young animal is situated dorsal to the base of the gills; from the ventral side one sees it covered by the roots of the branchial artery and vein. The opening of both oviducts projects only slightly into the mantle cavity, as is characteristic for all Oegopsida. Dissection of the juvenile oviduct (Figure 7) shows a short, slightly undulate tube which opens in the body cavity and ends between two spoon-shaped lips, a dorsal and a ventral one. The oviduct glands are situated in these lips. If it is assumed that the oviduct glands and their openings grow obliquely anteriorly during maturation until they become contiguous on the median surface of the abdomen, the condition described for *Abraliopsis* is obtained. Examination of 3 mature females of *Abralia* showed that this is in fact the case. The oviduct glands are situated close together but they are not so closely connected as in *Abraliopsis*. Nidamental glands were also absent in mature females of *Abralia*. So much mucus from the oviduct glands was secreted that it filled part of the mantle cavity. When this solidified mass was carefully removed, the condition resembled strikingly that in the female *Abraliopsis*, including the absence of nidamental glands.

95 **Measurements**

	Female from Station 256	Male from Station 254	Male from Station 54
Total length to tip of 4th arm	75 mm	50 mm	39 mm
Dorsal length of mantle	38 mm	26 mm	20 mm
Dorsal base of fins	24 mm	14 mm	—
Width of a fin	17.5 mm	11.5 mm	10.5 mm
Width of head	14 mm	—	10 mm
Greatest width of mantle	15 mm	12 mm	—
Length of 1st arm	22 mm	—	—
Length of 2nd arm	27 mm	—	—
Length of 3rd arm	25 mm	—	—
Length of 4th arm	28 mm	18 mm	14 mm

Postembryonic development of *Abraliopsis*

(Plates VI and VII)

I obtained an almost continuous series of the postembryonic development of *Abraliopsis*, and I could prove that a character of the adult animal is already distinct in very young larvae little longer than 3 mm. Still younger stages can be determined as belonging to this genus with some probability, although this character is absent. It is therefore advisable to describe the oldest stages first and to trace the development back from the oldest to the youngest stages. This will show more distinctly that the young stages definitely belong to the cycle of development of *Abraliopsis*, although they have a markedly different habitus.

We begin with a young stage of *Abraliopsis*, caught with a vertical net at Station 54 near the Guinea Current (Plate VI, Figure 2). Its measurements are as follows:

Total length to tip of ventral arms	20 mm
Dorsal length of mantle	11 mm
Width of head at level of lens of eye	5 mm
Length of dorsal base of fins	5.6 mm
Width of both fins together	10 mm
Length of ventral arm	8 mm
Length of 2nd arm	7 mm
Length of 3rd arm	6.5 mm
Length of 1st arm	5.2 mm

96 This young specimen resembles the adult in its general form, although the proportions of the body are slightly different. The presence of the 3 black knobs on the ventral arms is characteristic for the genus. The large fins are longer than half the mantle and taper sharply toward the posterior end of the body. The global-shaped mantle and the funnel are muscular; the funnel extends to the lower quarter of the eye.

The arms are strongly developed. The dorsal arms bear 5 proximal and about 7 distal pairs of suckers; their swimming membrane forms a weak keel at the distal end. The 2nd arms bear 6 proximal pairs of hooks and 6–7 distal pairs of suckers; they, too, are fitted out with a weak swimming membrane at the tip. The 3rd arms bear 8 pairs of hooks and about 8 pairs of suckers at the distal end, and the swimming membrane is well developed. The ventral arms, which end in 3 black knobs, bear 11 pairs of relatively widely separated small hooks and about 4 pairs of widely spaced suckers distally; a keel is absent.

The tentacles are strongly developed but their clubs show some juvenile characters. The membranes form only narrow ridges, and the transformation of suckers into hooks is not as far advanced as could be expected from comparison with a young specimen which is described below.

The carpal part is well differentiated and consists of 4 suckers on the left tentacle and 5 on the right; 5 and 4 indistinct knobs are situated between the suckers.

The proximal part of the hand bears 2 large medioventral and 2 small mediodorsal hooks on the left club, and 3 large medioventral and 2 small mediodorsal hooks on the right club, one of which still resembles a sucker. The dorsal marginal row of suckers is well preserved but only the proximal sucker of the ventral row persists. The hand part bears numerous suckers in rows of four.

The tentacle is vividly pigmented on the outer side of the club; a row of chromatophores extends along the stalk.

The eyes are large and slightly protruding; below them are the two olfactory tubercles, flnaked by two weakly developed folds.

The luminous organs are symmetrically arranged. The skin organs form 4 ventral rows on each side of the mantle; the outer row is markedly lateral in position and consists of 4 widely spaced organs. The dorsal side of the mantle and the other parts of the body have no luminous organs. Numerous younger luminous organs are present as small white dots between the older, more developed and more strongly pigmented organs. The 3 pairs of ventral rows continue on the funnel, where the outer rows are only indicated by 2 slightly covered organs. The head bears 5 rows of skin organs, a median and 4 lateral rows. The outer lateral row surrounds the iris, and the inner lateral row passes at the level of the inner margin of the eye and continues on the dorsal edge of the ventral arms. The ventral
97 edge also bears organs which are formed by a bifurcation of the median row. The 3rd arms bear only a few organs in a loose uniserial arrangement.

Some of the eye organs are visible distinctly through the skin. As in the adult animal, there are 5 organs on each eye in this stage; the terminal organs are much larger than the 3 inner ones.

The coloration of this young stage is less vivid than in the adult. The chromatophores are strictly symmetrically arranged. The chromatophores on the head and mantle are prominent. The head bears two large dorsal chromatophores at the level of the middle of the eyes; between them extends a median row of 4 smaller chromatophores. Two other chromatophores are situated laterally behind the eyes. The head bears a horizontal row of 4 dark chromatophores at the level of the middle of the eye on the ventral side. The arrangement of the other chromatophores is shown in the figure; there are also 2 strongly pigmented chromatophores laterally below the base of the fins at the posterior end of the body.

This description of the oldest juvenile stage of *Abraliopsis* agrees well with Pfeffer's diagnosis (1900, p. 165) of the genus *Micrabralia*: "... luminous organs arranged in 6 rows, forming two medium longitudinal stripes of numerous tubercles and 4 lateral rows of isolated tubercles; fins terminal; hand part of tentacle with 2 rows of hooks and one row of suckers; arms only with hooks, ventral arms with a clublike swelling at the tips."

Pfeffer (p. 167) considers it possible that *Micrabralia* belongs to the developmental cycle of *Abraliopsis* into which it fits quite naturally. The generic name can therefore only be used as a symbol for a juvenile stage, i.e. the *Micrabralia* stage.

A slightly younger stage which forms a transition to the *Compsoteuthis* stage closely resembles the *Micrabralia* stage.

The measurements of a specimen caught with a vertical net at Station 223 in the Indian countercurrent (near the Chagos Archipelago) are:

Total length of ventral arms to tips	15	mm
Dorsal length of mantle	7	mm
Width of head	4	mm
Length of dorsal base of fins	3.2	mm
Length of 4th arm	7	mm
Length of 2nd arm	6.5	mm
Length of 3rd arm	6	mm
Length of 1st arm	5.5	mm
Length of tentacle	11	mm

Corresponding to its smaller size, this specimen (Plate VI, Figures 3, 4) shows a number of
98 characters which are transitional to the juvenile stages. It is without doubt an *Abraliopsis* because of the presence of 3 black knobs at the tips of the ventral arms. On the other hand, both ventral arms are without hooks and have only small, loosely arranged suckers. Hooks are present, however, on the other arms. The 1st arm bears 9 hooks followed distally by 5 pairs of suckers. The 2nd arm bears 6 pairs of hooks and a number of suckers at the tip. The 3rd arm bears 13 hooks (about 7 pairs) and also a number of suckers at the tip. The keel-shaped swimming membrane, which is so well developed in the older stages, is still absent.

The **tentacle club** resembles that of older stages in its large number of hooks. It bears 4 carpal suckers but still no knobs between them. The proximal hand part has 2 rows of hooks, formed by transformation of the proximal suckers of the median rows. The medioventral row of both clubs consists of large hooks; the mediodorsal row consists of 2 small hooks. The ventral marginal row is absent, but the dorsal row persists. The distal part of the hand bears the usual quadriserial rows of suckers. The retarded condition of the hooks in the *Micrabralia* stage shows that the transformation of suckers into hooks is variable and not strictly parallel to the general growth.

It is remarkable that the olfactory tubercles and the folds are still absent, even as "anlagen".

The luminous organs form 8 rows on the mantle, of which only 4 are distinct. The rows adjacent to the ventral midline consist of about 10 symmetrically situated organs between which are white dots which are developmental stages of additional organs. The next row consists entirely of such dotlike, unpigmented organs. The 3rd row, which ends at the mantle corner, is more distinct as it consists of 3 or 4 pigmented organs. The 4th row is situated quite lateral (Figure 4), with 3 weakly pigmented organs. Only 2 fully developed organs are present on the funnel. The head bears a median row of 3 developed organs, flanked by two lateral rows with a single organ. The dotlike "anlagen" of additional organs, 4 on each ventral arm, are distinct.

The distribution of chromatophores is about the same as in the previously described stage.

The young stages described below differ from the older larvae mainly in having no hooks on the arms. I call them the *Compsoteuthis* stage, because there is only one row of hooks on the club and they would therefore belong to Pfeffer's genus *Compsoteuthis*. A specimen from the Atlantic South Equatorial Current (Plate VI, Figures 5, 6) belongs to this stage. Its measurements are:

	Dorsal length of mantle	4.5 mm
99	Dorsal length of fins	1.5 mm
	1st arm	3 mm
	2nd arm	5 mm
	3rd arm	4.5 mm
	4th arm	2.5 mm

The above measurements indicate that the relative lengths of the arms change. The formula here is: 2, 3, 1, 4, compared with 4, 2, 3, 1 in the older stages and the adult. Although all the arms bear suckers, the identity of the specimen as *Abraliopsis* can be recognized by the single knoblike terminal swelling on each ventral arm, instead of 3 knobs. Since such knobs are absent in all other Enoploteuthidae, this apparently minor character is important for the determination of the genus. Another character of *Abraliopsis* is present on the tentacular club, which bears only two hooks in the ventral median row in the proximal part of the hand, and otherwise only suckers. The 5 carpal suckers are not yet

separated from the hand part, and the proximal sucker of the ventral marginal row is still present.

The fins of this stage are relatively smaller, barely one third of the mantle length, with rounded outer margin.

Each eye bears 3 distinct luminous organs, which apparently correspond to the middle and the two outer of the 5 organs of the adult. The skin organs are still markedly underdeveloped and are arranged in two rows on each side of the mantle. The middle rows consist of 3 symmetrically situated, slightly pigmented organs, the outer rows of only two whitish, underdeveloped organs. The other skin organs are distributed as follows: two on the funnel, one on each eye and one on each ventral arm.

This stage certainly belongs to *Abraliopsis*, as shown by a slightly older larva from the Indian Countercurrent (Plate VII, Figure 1). The knoblike swellings of the ventral arms are asymmetrically developed; because there is only one such swelling on the right ventral arm. The measurements of this stage differ little from those of the larva described above:

Dorsal length of mantle	5 mm
Width of head	3 mm
Dorsal length of fins	1.8 mm
1st arm	3.5 mm
2nd arm	4.5 mm
3rd arm	5.5 mm
4th arm	3 mm

All arms bear only suckers at this stage.

The carpal part of the left club (Plate VII, Figure 2) bears 5 suckers and borders close to the hand part, as in the larva described above. The hand part has a row of 3 hooks formed from suckers of the ventral median row. The mediodorsal and dorsal rows form a long stripe on the proximal hand part with the suckers arranged in a slightly zigzag row. Only one proximal sucker of the ventral marginal row is present, next to the first hook. The distal hand part bears the usual 4 rows of suckers, which rapidly decrease in size.

100 There is no indication of olfactory tubercles or the folds which surround them.

The luminous organs on the mantle are slightly more numerous than in the previously described larva and form 4 rows on the ventral side. There is still no indication of the two lateral rows, which appear later. Isolated organs are present on funnel and head, and two on each ventral arm.

The chromatophores are sparsely developed; 5 chromatophores on the dorsal side of the head are distinct, one of them in the middle, the other 4 symmetrically arranged.

As in the preceding larva, the genus of this form is determined by the formation of the tentacle club, the arrangement in rows of the mantle luminous organs and especially by the presence of a knoblike swelling on one of the ventral arms. However, this larva differs from the later stages in a number of characters, mainly the relative lengths of the arms, the absence of hooks on the arms and the small fins.

As noted above, both larvae fit Pfeffer's diagnosis of the genus *Compsoteuthis* (Pfeffer, 1900, p. 165). They exhibit a more primitive character only because the transformation of suckers into hooks has not yet begun.

To the descriptions of the *Compsoteuthis* stage I add that of a number of younger larvae which undoubtedly belong to the developmental cycle of *Abraliopsis* but differ from the older forms in the absence of hooks on the club.

One of them, caught in the Indian Countercurrent, has the following measurements (Plate VII, Figures 3 and 4):

Dorsal length of mantle	3.3 mm
Width of head	1.5 mm
Length of 1st arm	2.5 mm
Length of 2nd arm	3.8 mm
Length of 3rd arm	3 mm
Length of 4th arm	2 mm
Length of tentacle	5 mm

The arm formula is thus: 2, 3, 1, 4. The larva belongs to *Abraliopsis* because of the presence of one knoblike swelling at the tip of each ventral arm, although the swelling still lacks the dark pigment. Another character of the genus is the arrangement of the 6 luminous organs on the mantle in two strictly symmetrical longitudinal rows of 3 organs each. Two organs are present on the funnel; other luminous organs are absent.

The club of this specimen (Figure 5) shows a typically young larval arrangement of suckers. There are 5 proximal suckers, which probably belong to the carpal part. They are followed by an irregularly biserial arrangement of 11 suckers, one of which is large and apparently on the verge of being transformed into a hook. The distal part of the still short club bears about 5 quadriserial rows of suckers.

101 The fins are small, situated at the posterior end of the body; they form an oval together and do not taper posteriorly.

The knoblike swelling of the ventral arms is already recognizable in smaller larvae of only 2 mm dorsal mantle length (Figure 6). As in the older stages, this swelling is situated proximal to the delicate tip, which is usually bent almost at a right angle. The ventral arms of these forms are also much shorter than the other arms: they are 1 mm long, the 2nd arms 2 mm and the tentacles 2.6 mm. The arms and clubs bear suckers only. The two dorsal muscular plates of the mantle diverge markedly anterior to the tip of the body, and the bases of the delicate, spatulate fins, therefore, diverge more strongly than in the older larvae. Luminous organs are still absent at this stage. This larva was caught in the Indian Countercurrent.

The youngest larva which belongs to *Abraliopsis* with certainty (Figure 7) was also caught in the Indian Countercurrent; it is only 4 mm long and its dorsal mantle length is 2 mm. The ventral arms are very small, but each terminates in a whitish knob.

The arm formula is 2, 1, 3, 4. This is the condition of the newly hatched larva. The two dorsal pairs of arms are much larger than the ventral arms. The club (Figure 8) is very short, with 5 proximal suckers in the carpal part and with 6–7 quadriserial rows in the hand part, which consist of suckers of gradually decreasing size.

Luminous organs are absent. The very small fins are situated at the margin of the muscular plates, which diverge broadly posteriorly.

A number of larvae resemble the above larvae of the *Compsoteuthis* stage; they have the same characteristics, but the typical knoblike swellings on the ventral arms are absent and it is therefore not certain that they belong to *Abraliopsis*. They may be larvae of *Abraliopsis* in which some characters are undeveloped; however, they may also belong to the related genus *Enoploteuthis*, or perhaps to *Abralia*.

An example of this group is a specimen caught in the Indian North Equatorial Current (Plate VII, Figures 20, 21). This larva closely resembles the *Compsoteuthis* stage shown in Figure 1, but is apparently slightly younger. The dorsal mantle length is 4.3 mm, the total length 9 mm (to the tips of the 4th arms) and the head is 2.5 mm wide. Olfactory tubercles are recognizable but not distinct and are surrounded by weak swellings. The fins are spatulate and very small, 1 mm long and 1.3 mm wide.
102 The arms are well developed; formula: 2, 3, 4, 1. All arms bear suckers only; the first arms are 2 mm long, the following pairs 3.2, 3 and 2.8 mm, respectively. Only the 3rd arms have a weak swimming membrane.

The **tentacle club** bears suckers only (Figure 22). The carpal part consists of about 4 proximal suckers and is united with the hand part, which, except for the first two suckers, immediately forms quadriserial rows of suckers; this differs from the proximal zone of the hand part of the *Compsoteuthis* stages, in which the rows are biserial (Figures 2, 5). A weak protective membrane is already present on the dorsal margin.

The **luminous organs** on the eyes are distinctly developed; there are 5 on the ventral side of each eyeball. The posterior (lower) organ is the largest, the middle organ slightly larger than the others.

The **skin organs** resemble those of the *Compsoteuthis* stage (Figure 1). They form 3 longitudinal rows on each side of the mantle and a few organs are situated laterally. As shown in Figure 20, other organs are situated on the ventral side of the head, the eyelid, and the 4th pair of arms.

The **chromatophores** are numerous. They form about 4 rows on the ventral side of the mantle; two large chromatophores are situated at the posterior end of the body. The head bears dorsally 6 large, symmetrically arranged chromatophores (Figure 21).

Figure 23 shows a slightly younger larva which also has no knobs on the ventral arms. It was collected in the same locality as the former larva (Station 218, Indian North Equatorial Current) and corresponds to the stages shown in Figures 3 and 4. A more detailed description is therefore unnecessary; it may be mentioned only that there are 4 symmetrically arranged luminous organs on the ventral side of the mantle.

Of great interest are a number of still younger stages which lead back to freshly hatched larvae. The larva shown in Figure 9 corresponds to that shown in Figure 7. Both were collected in the Indian North Equatorial Current; the larva in Figure 9 differs from that in Figure 7 only in the absence of the minute knoblike swellings of the ventral arms. Arm formula: 2, 3, 1, 4.

The same catch in the Indian North Equatorial Current (Station 217) contained still younger stages with a dorsal mantle length of only 1.5 mm (Figure 11). Only the dorsal arms, tentacles and the 2nd arms are distinct in this stage; the 3rd and 4th arms are represented only by small knobs. The club (Figure 10) bears only 9 suckers, arranged in rows of two. The muscular plates of the mantle diverge widely posteriorly so that the fins are also widely separated.

The youngest larva known to me is shown in Figure 12 under higher magnification. This specimen,
103 caught in the Guinea Current, is 1.7 mm long and has a dorsal mantle length of 1 mm. Its mantle extends far anteriorly, ending just behind the distinctly oval eyes. The arm apparatus consists of the tentacles and the 1st and 2nd arms. The tentacles resemble the arms so closely that only the minute knoblike "anlagen" of the 3rd and 4th arms give an indication of the true nature of the tentacles. Each tentacle (Figure 13) bears only 5 suckers, one of them proximal, the others in two distal pairs. As noted on p. 12, these suckers will form the carpal part of the club. There are 4 suckers on each arm. The fins are very small in relation to the mantle.

The **chromatophores** are sparse. The head bears two median dorsal and two pairs of lateral chromatophores; one pair of chromatophores is situated on the mantle anterior to the fins and 3 chromatophores are situated on each tentacle but none on the arms.

It is difficult to decide whether these very young larvae belong to the developmental cyle of the Enoploteuthidae. It will be noted later that the youngest larvae of other families of Oegopsida also have only 3 pairs of arms including the tentacles, and their ventral arms are represented by small knobs.

Except for the youngest larvae, the larvae of *Abraliopsis* which can be identified with certainty have a relatively slender body and an early well-developed arm apparatus in which the ventral arms are at first shorter than the others. The most important character of the genus, the knoblike swellings, is already present in these stages. The 4th arms later become longer than the other arms and develop two additional terminal knobs. The transformation of suckers into hooks begins at the base and proceeds distally; the suckers of the 4th arms persist longest.

The **club** is narrow from the beginning. It bears a varying number of biserial suckers in the proximal part, followed after an interval by quadriserial rows of 4 suckers. A transformation of some suckers into hooks in the proximal part begins in the later stages, at first in the medioventral row and later in the mediodorsal row. The hooks on the tentacles appear before those of the arms.

The **luminous organs** on the eyes apparently develop before those of the skin. The latter appear first on the mantle, forming a strictly symmetrical pattern of longitudinal rows, of which the median rows develop before the lateral rows. The ventral arms bear at first one row, later two rows of luminous organs.

The fins of the youngest larvae are very small, spatulate, wider than long. They become gradually longer, triangular and form together a rhombus which tapers sharply toward the posterior end of the body.

The neck folds and olfactory tubercles develop at a much later stage.

104

OTHER LARVAE OF ENOPLOTEUTHIDAE

1. A Larva of *Thelidioteuthis alessandrinii* VÉR.

(Plate VII, Figures 16, 17)

Loligo alessandrinii VÉRANY, 1851 p. 99, Plate 35, Figures f, g, h.
Enoploteuthis polyonyx TROSCHEL, 1857, p. 67, Plate IV, Figure 9.
Abralia megalops VERRILL, 1882, p. 364; 1883, p. 105, Plate III, Figure 4; 1884, p. 143, Plate XXVIII, Figure 2, Plate XLIV, Figure 2.
Enoploteuthis pallida PFEFFER, 1884, p. 18, Plate III, Figures 23, 23b, 23c.
Calliteuthis alessandrinii APPELLÖF, 1889, p. 27, Figures 7–11.
Thelidioteuthis polyonyx PFEFFER, 1900, pp. 165, 167.

A vertical net sunk to a depth of 2,000 m at Station 235 in a branch of the Indian South Equatorial Current caught a larger larva which undoubtedly belongs to *Thelidioteuthis*.

This larva has a dorsal mantle length of 5.5 mm. It resembles the older larvae of *Abraliopsis* in the well-developed arm apparatus and the relatively large fins. It differs in its blunt posterior end and in the retarded development of the 4th arms. Arm formula: 2, 3, 1, 4. The fins are rounded, 1.4 mm wide, with large, broadly diverging dorsal bases. The funnel cartilage is long, narrow, with a median groove into which the rodlike mantle cartilage fits.

The arms bear suckers, and there is no trace of transformation into hooks. This applies also to the tentacular club (Figure 17), which bears a single proximal sucker, followed by 3 pairs of larger suckers and then 3 small suckers; further distally are a number of irregularly arranged suckers which do not form rows of four. The marginal suckers are larger than the median suckers.

Numerous chromatophores cover the ventral side of the body. The head bears dorsally a median group of 4 chromatophores, flanked on each side by two lateral pairs of chromatophores.

Only 4 luminous organs are present, one pair in the middle of the ventral side of the mantle, the other pair at the level of the eyes. Eye organs are absent, as we found after removal of the lid fold.

This larva undoubtedly beongs to *Thelidioteuthis alessandrinii* Vér., a species described under various names. Its identity becomes clear by comparison with the youngest stage of this species
105 known, *Calliteuthis alessandrini* Appellöf, which has similar eyes. Both have a rounded posterior end and sparse luminous organs, nearly identical forms of fins and ventral arms which are shorter than the other arms. The form of the club is decisive: the marginal suckers of the hand part are larger than those of the median rows. Appellöf's specimen closely resembles in this respect that of Vérany, which is only slightly larger. My larva is only half as large, and much less developed, with only 4 luminous organs and very small ventral arms.

I have accepted Pfeffer's synonymy for this species, but it must be realized that the early descriptions are too brief and not clear on some points; they need revision. This applies especially to the arrangement of the luminous organs and the form of the club. The luminous organs of this larva are surrounded on the inner side by 4 large chromatophores; sections of one of these organs showed that it is still not completely developed. The pigmented envelope of chromatophores is followed by a system of lamellae with numerous nuclei which are present to the periphery. The organ resembles in general a juvenile organ of *Abraliopsis*.

The description of the left club of the adult animal by Troschel suggests that the dorsal row of suckers in the proximal zone of the hand part is suppressed, while the ventral row persists. This condition does not agree with the condition in other Enoploteuthidae. Moreover, stages which show the gradual transformation of suckers into hooks are still not known.

The developmental cycle of *Thelidioteuthis* possibly includes a number of younger larvae, one of which is shown in Figure 14. This specimen was caught in the Indian North Equatorial Current. It has a dorsal mantle length of 2.8 mm. Its arm apparatus is well developed, except for the short, ventral arms which form only short stumps.

The **club** (Figure 15) bears an isolated proximal sucker, followed by 4 others (two larger and two smaller); further distally are about 3 rows of 4 suckers. Luminous organs are absent, particularly those on the eyes. The fins are terminal, small and spatulate.

The **chromatophores** are again numerous on the ventral side. The head bears dorsally 6 chromatophores, two of them median, the others forming two lateral pairs.

Figure 18 shows a slightly smaller larva from the Indian Countercurrent (Station 223), with a dorsal mantle length of barely 2 mm and the arm formula 2, 1, 3, 4. The 3rd and 4th arms form short stumps. As in the preceding stage, the arms bear suckers; the club has an isolated proximal sucker, followed by a few biserial suckers which gradually decrease in size toward the tip (Figure 19).

The youngest larva which probably belongs here was caught in the Canaries Current (Figure 24,
106 Station 54). It is 3.5 mm long and has a dorsal mantle length of 1.7 mm. The arm formula is 2, 1, 3, 4, as in the last-mentioned stage. The arms bear few but distinct suckers; the club (Figure 25) also shows

a proximal sucker, followed by a biserial arrangement of about 6–7 pairs of suckers which decrease gradually in size to the tip. The terminal fins are very small. All chromatophores of this specimen were strongly contracted.

2. Indeterminable Larvae of Enoploteuthidae

(Plate XIII, Figures 13–23)

In the description of the young stages of *Abraliopsis* and *Thelidioteuthis* we mentioned a number of larvae which could not be placed with certainty in one of the two genera. This applies not only to the freshly hatched larvae in which specific characters are still absent but also to some older forms; the connecting stages to the adult are not known.

I will therefore only describe a group of indeterminable larvae of Enoploteuthidae from the Cape area.

The oldest of these stages (Figure 13, Station 91) has the characteristic of a larva of *Abraliopsis* but differs in having no luminous organs or knobs on the ventral arms. The dorsal mantle length of this specimen is 4.5 mm; the head is 2.4 mm wide at eye level. The well-developed arm apparatus bears only suckers, but the club already shows two distinct hooks (Figure 14). The carpal part bears about 5 suckers; it merges with the hand part, in which two suckers of the medioventral row are transformed into hooks.

The larva has no luminous organs, although hooks are already present on the club. It can therefore not belong to the developmental cycle of *Abraliopsis* or *Thelidioteuthis*. Older stages would have to be examined to determine the genus of this larva, but its characteristic form and the structure of the funnel cartilage clearly show that it belongs to the Enoploteuthidae.

A younger larva of the same catch (Station 91) (Plate XIII, Figure 15) probably belongs to the developmental cycle of the above specimen. The dorsal mantle length is 3 mm; the fins are terminal, very small and the 3rd and 4th arms form only short stumps. The arm formula is 2, 3, 1, 4. The club (Figure 16) bears 5 proximal suckers—the future carpal part—and about 6 transverse groups of quadriserial suckers. Luminous organs are absent.

At the neighbouring Station 102 I obtained a number of larvae which resemble the larva described above. As the illustration of 3 of the larvae shows (Figures 17, 19 and 20), they are generally plumper
107 than the youngest stages of *Abraliopsis*. Their length is 3.8–4 mm, the dorsal mantle length is 2.4 mm. The 3rd and 4th arms form small knobs; the fins are small and widely separated because of the wide dorsal divergence of the muscular plates. The ventral side of the mantle is colorless, in contrast to the vivid pigmentation of the stage described above. All specimens bear 6 dorsal chromatophores on the head, two are median and two pairs lateral. There are 4 pairs of chromatophores on the dorsal side of one specimen, one pair directly anterior to the fins. The other specimens had no pigmentation on the dorsal side.

The **clubs** (Figures 18 and 21) are short and plump and resemble those of the preceding stage. There are 5 proximal suckers which are also followed by rows of 4, but in smaller numbers.

Another larva found at the same station (102) closely resembles these forms, despite its small size, and perhaps represents the youngest stage of the whole group (Figure 22). Its length is 2.7 mm and the dorsal mantle length is 1.8 mm; it has 3 pairs of arms of which the longer develops into tentacles (Figure 23). The 3rd and 4th arms form short processes; the arms are 0.3 mm and the tentacles 0.7 mm long. Only a few pairs of suckers are present on the arms; the club more or less

resembles that of the older stages. The eyes are round. Luminous organs are absent, but the pigmentation is vivid. There are 5 transverse rows of numerous chromatophores on the ventral side and 4 median and 2 lateral pairs of chromatophores on the dorsal side. There are only 3 chromatophores on the dorsal side of the head, one single and two paired; only one pair of relatively large chromatophores is visible on the ventral side but is partly covered by the mantle.

Enoploteuthis leptura
(Plate XI, Figures 5, 6)

Loligo leptura LEACH, 1817, *Misc.*, Vol. III, p. 141; sp. 21; "*Tucky*" *Exped.*, *Zaire*, IV, p. 411, Plate XVIII, Figures 3, 4.
Loligo smithii LEACH, 1817, *Misc.*, p. 141, sp. 3.
Enoploteuthis leptura FÉRUSSAC and D'ORBIGNY, 1835–1842, p. 337: *Onychoteuthes*, Plate II, Figures 3, 4: Plate IV; Plate XI, Figures 6–14; Plate XII, Figures 10–24.

Because of the interest of the new discovery of this forgotten species by the German South Polar Expedition, I obtained the permission of Prof. VANHOEFFEN to reproduce an illustration. I shall give a more detailed description in the report of the expedition. Only the diagnosis of the genus is given here (p. 49). Figure 6 is an exact drawing of the slightly injured left club, the only one present. The medioventral row of the club contains 7 hooks, one of which id displaced dorsally. Only 3 hooks are still present in the mediodorsal row, the other 4 are lost. The condition of the club agrees with the
108 diagnosis: proximal part of the hand with 7 large medioventral hooks and 7 small mediodorsal hooks; marginal rows of suckers suppressed.

This specimen, a young male, was caught in the South Atlantic. It was severely damaged; the ventral arms, which are straight in another specimen are curved like a lyre in the illustrated animal.

Tribe II: Pterygiomorphae CHUN

Pterygioteuthis H. FISCHER, 1895

There are two species of *Pterygioteuthis*, one of them new. The differences between them are as follows:

First, 2nd and 3rd arms with paired hooks in the middle part. Club with two carpal suckers. Ventral arms without suckers or hooks. Hectocotylus (left ventral arm) bare, with large swimming membrane and two large glandular pads which consist of long tubes. The proximal pad extends from the base to the middle of the arm and is colored red; the distal pad is short. Between the pads is a striated chitinous lamella with two spine-shaped teeth. Fifteen luminous organs on each eye.

Pt. giardi FISCHER

A few (4–5) median suckers of the ventral row on the 1st, 2nd and 3rd arms are transformed into hooks. Club with 3 carpal suckers. Ventral arms with small paired suckers their whole length, which are almost uniserial on the right ventral arm of the male. Hectocotylus bare,

with large swimming membrane and two glandular parts of about equal size, between which is a finely toothed chitinous plate. Fourteen luminous organs on each eye.
Pt. gemmata n.sp. South Atlantic

Pterygioteuthis giardi H. Fischer
(Plates XII, XIII, XIV, XV, XVI)

Pterygioteuthis giardi H. Fischer, 1895, p. 205 (pp. 5–11) Plate IX.
Pterygioteuthis margaritifera Rüpp. juv. Pfeffer, 1900, p. 166.
Pterygioteuthis sp. Chun, 1903, p. 72 (luminous organs); 1904, p. 243 (hectocotylus); 1905, p. 645 (male genitalia).
Pterygioteuthis giardi Hoyle, 1904, pp. 39, 51, Plates VII, VIII.
Pterygioteuthis giardi Fischer and Joubin, 1906, p. 334, Figures 6–8; Plate XXIII, Figures 6, 7; Plate XXIV, Figures 9–15.
Pterygioteuthis Marchand, 1907, p. 26 (male genitalia).
Pterygioteuthis giardi Chun, 1908, p. 87.

Localities: Station 215. The smallest male. Indian North Equatorial Current, 7°1′ N, 85°56′ E. Vertical net to 2,500 m.
Station 217. Two medium-sized males. Indian North Equatorial Current, 4°56′ N, 78°15′ E.
Station 218. Large male. Indian North Equatorial Current, 2°29′ N, 76°47′ E.

109 Although the genus has repeatedly been described, most recently by Hoyle (1904), it seems to be indicated to present a new description of *Pterygioteuthis*. On the one hand, the authors omitted a number of important characters; on the other, Hoyle separated the Mediterranean species *Pterygioteuthis margaritifera* as the representative of a new genus, *Pyroteuthis*. I did not consider this separation as justified at first. However, I found later a number of characters not known to Hoyle, which make the establishment of a new genus advisable.

Form of body. The body is slender with pointed posterior end which projects markedly beyond the relatively well developed fins. The head is wider than the mantle because of the large eyes. Arms and tentacles are of moderate length, and the dark buccal funnel is very long. The body has a fleshy consistency.

Pyroteuthis and *Pterygioteuthis* are so similar externally that they may be mistaken for each other. Both genera belong to the smaller Cephalopoda; they are sexually mature at a total length of only about 50 mm. *Pyroteuthis* is slightly larger than *Pterygioteuthis*. I concluded this from an examination of two specimens from Messina which are 90 mm long (including the tentacles) and in which the dorsal mantle length is 34 mm.

The dorsal length of the **mantle** is 17 mm in the largest male of *P. giardi* examined (Plate XIV, Figure 1). Its dorsal surface descends in an elegant curve (Plate XII, Figure 3) to the spine-shaped posterior end, which projects 3.3 mm behind the base of the fin in the large male. The dorsal corner of the mantle is blunt in young and pointed in older specimens; the ventral corners are always distinct.

The **fins** are rounded or oval; they taper toward their dorsal base (Plate XII, Figure 1). The fins do not reach the pointed end of the body; their dorsal bases are widely separated. The transverse width of both fins together is about half of the mantle length. The moderately large funnel extends to the level of the posterior margin of the lens.

The **head** is wider than the mantle. The eyes are large and apparently do not attain their full size before sexual maturity. Neck and occipital folds are absent, but the small olfactory tubercles are well developed.

The **arm apparatus** is moderately developed and there is only little difference between the length of the arms. These proportions apparently change according to age and sex. In contrast to the data of Hoyle, I found that the 3rd arms are always the longest, followed closely by the 4th arms; then follow the 2nd arms and finally the 1st arms. Formula: 3, 4, 2, 1. All arms have external swimming membranes which are raised to a high keel distally, particularly on the 3rd arms. The **swimming membrane** at the
110 base of the ventral arm forms a wide, transparent lamella which extends over the tip of the tentacle and reaches to the proximal part of the swimming membrane of the 3rd arm (Plate XIII, Figure 3).

The **protective membranes** are also well developed. The first 3 pairs of arms have small dorsal protective membranes but the ventral protective margins are very large and are supported by cirriform muscular bridges which alternate regularly with the suckers (Plate XIII, Figure 2). The protective membranes of the ventral arms are only weakly indicated. In a young male of *P. giardi*, the protective membranes of both dorsal pairs of arms are widened in the middle and fused so that they connect the dorsal pairs of arms and extend toward the ventral arms (Plate XIII, Figures 5 and 7). Pfeffer apparently observed such a condition, because he considers it as characteristic for the genus. However, this condition is not distinct in the mature specimens but is effaced by the large development of the buccal funnel (see below).

It is characteristic for the genus that only a limited number of **suckers** in the middle of the arm are transformed into **hooks** in old animals. I was able to determine this more exactly after the discovery of a new species of *Pterygioteuthis*, *P. gemmata*, caught at night on the surface in the South Atlantic (South Polar Expedition). The hooks in *P. giardi* are arranged in pairs formed by the transformation of a limited number of median dorsal and ventral suckers on the first 3 pairs of arms. In *P. gemmata*, the hooks are single and only a few ventral suckers are transformed. As an example, we describe the larger specimen of the previously unknown male of *P. giardi*. The dorsal arms have 3 pairs of proximal suckers and one single sucker. These are followed by 7 larger hooks, one of them single, the others in 3 pairs. Further distally are 4 or 5 pairs of smaller hooks, followed by 13 pairs of suckers which gradually decrease in size, the last of them very small. The dorsal arms thus bear about 20 pairs of suckers and 8 pairs of hooks. The male has thus apparently more numerous hooks than the female illustrated by Hoyle (1904, Plate VII, Figure 7). This is similar in the young male the arms of which are illustrated on Plate VI, Figure 2. This specimen has 5 pairs of proximal suckers, followed by 14 hooks (7 pairs), including 3 large proximal suckers; the end of the arms again bears paired suckers.

The proximal part of the 2nd arms bears 3 pairs of suckers, followed by two pairs of hooks. The distal ventral hook is very large. The apex of these arms is without suckers. A similar condition is present in the younger male (Plate VI, Figure 2), i.e. 3 hooks, including a large ventral hook.

111 The 3rd pair of arms has only 2 proximal suckers, followed by 3 pairs of hooks; the tip is also without suckers. In the younger male, these arms have fewer hooks and a correspondingly larger number of suckers which are arranged as follows: 5 ventral and 2 dorsal suckers and two dorsal hooks on the left arm (Figure 2); there is a ventral hook in addition to the two dorsal hooks on the left arm.

P. giardi thus has the following armature of suckers and hooks on the first 3 pairs of arms (including the female described by Hoyle): there are numerous suckers and hooks, and numerous pairs of suckers in the distal part on the dorsal arm which are absent on the other arms; there are fewer suckers and hooks on the 2nd and 3rd arms and distal pairs of suckers are absent.

The ratio between suckers and hooks is variable, as shown by the arms of the smallest male (Station 215, Plate XII, Figure 3, 4). The distal paired suckers on the dorsal arms are still not developed, but the left dorsal arm has 3 and the right 4 pairs of hooks distal to 5 pairs of proximal suckers. The 2nd and 3rd arm bear more hooks than the older stages: 3 and 5 pairs respectively. There are 3 small distal

suckers on the right 3rd arm. This suggests that the distal pairs of suckers begin to disappear after formation of the hooks proximal to them.

According to HOYLE, the ventral arms of the female of *P. giardi* are without suckers and hooks. As I had only males, I shall describe the peculiar condition of the ventral arms in connection with the hectocotylization.

I did not find distinct differences between males and females of *P. gemmata* and the description of the species is therefore based on the largest female.

The dorsal arms of *P. gemmata* bear 23 pairs of suckers. Four ventral suckers of the 7th–10th pair are transformed into hooks. The second arms bear 14 pairs of suckers, of which 4 ventral suckers of the 6th–9th pairs are also transformed into hooks. The suckers of the 3rd arms also form 14 pairs, of which 5 ventral suckers of the 4th–8th pair are transformed into hooks.

The ventral arms of the female are without hooks, but the pairs of suckers persist throughout life. They form two rows with 16–17 pairs on both ventral arms in the 2 largest females and are more loosely arranged than on the other arms.

The male of *P. gemmata* shows a similar pattern, except for the ventral arms, which will be described below. The dorsal arms of the largest male bear 3 hooks, the 2nd arms 4 and the 3rd arms
112 5 hooks. It thus differs from the female only in that there is one additional hook on the 2nd and 3rd arms.

The **tentacles** are very short and pointed because the club is only slightly widened. The based part is curved like a lyre and has two spindle-shaped swellings (Plate XIII, Figures 1, 3; Plate XIV, Figure 1). The proximal swelling is covered by the membrane which is a continuation of the swimming membrane of the ventral arms toward the 3rd pair of arms. This swelling is slightly laterally compressed and lacks the intensively pigmented layer of chromatophores which is present on the outer distal swelling; the outer side is round in cross section (Plate XIII, Figure 3). The base of the tentacle of *Pyroteuthis* has the same form and enhances the similarities between the two genera. This character is of particular importance, because it is distinct already in the youngest stages and is the only character identifying the young forms of *Pterygioteuthis*, in which luminous organs are not yet developed.

Between the two swellings extends a thin membrane on the outer side of which pass a muscle and blood vessels. The membrane is easily torn in old specimens but not the muscle, which attaches the tentacle. This muscle is in no other Oegopsida as well developed as in *Pterygioteuthis*. It extends to the distal swelling and is visible as a narrow cord (Plate XIII, Figures 1, 3; Plate XIV, Figure 1). The slender muscles which attach the tentacles are united at the base of the ventral arms and descend deeply (Plate XIII, Figure 1).

The **club** was correctly described by FISCHER and HOYLE, who consider the absence of hooks as a primitive character. This applies also to the club of *P. gemmata*. HOYLE (1904, p. 42) separated the genus *Pyroteuthis* from *Pterygioteuthis* mainly because of the transformation of a few suckers into hooks on the club of *Pyroteuthis*. I would hesitate to establish a new genus on this character alone, if there were not far more important differences which became clear after the male of *Pterygioteuthis* was found. The club of a younger male of *P. giardi* bears two carpal suckers and two carpal adhesive knobs (Plate XIII, Figure 4). They are followed by a large number of suckers which soon form rows of 4 and gradually decrease in size toward the tip, without sharp differentiation into a proximal and a distal hand part. A protective membrane is still absent at this relatively young stage.

The club of *P. gemmata* differs mainly in the presence of 8 carpal suckers. This was the case in all specimens examined, males and females. The 8 adhesive knobs are usually indistinct, except in one of the oldest females. The hand part again consists of quadriserial rows of suckers. Adult specimens

have protective membranes, of which the dorsal membrane is markedly widened in the proximal half
113 of the club. A keel-shaped swimming membrane is present only in the distal part. There are 4 or 5 very large proximal suckers in the dorsal and mediodorsal rows.

The **buccal funnel** has to be described in more detail since it shows a number of characters which have so far been overlooked or wrongly interpreted. It is very large, dark violet, almost chocolate colored. The buccal membrane is supported by 8 buccal pillars and accordingly has 8 points. The dorsal pillars are situated so close together (Plate XIII, Figure 2) that Pfeffer mentions only 7 attachments. The inner surface of the buccal membrane has no villi but numerous radial, undulate, longitudinal folds. Cross sections show that the pigment is situated on the outer surface.

The attachment of the buccal membrane is characteristic. The protective membranes of the two dorsal pairs of arms widen in young specimens into a "sail" which connects the bases of the arms; this was also noted by Pfeffer. The "sail" is fused with the 6 dorsal points of the buccal membrane (Plate XIII, Figure 7). The two approximated dorsal points alternate with the 2nd and 3rd pairs of arms. This results in the formation of pockets at the two dorsal pairs of arms which are bordered by the outer surface of the buccal membrane and the inner surface of the arms. This condition persists also in the older stages, although the sail-like connections between the arms is gradually covered over by the buccal funnel during growth. The protective margins of the two dorsal pairs of arms pass into the outer surface of the buccal membrane, so that the pockets are maintained between the buccal membrane and the inner side of the arm bases. This is illustrated diagrammatically in Text Figure 21, which shows a cross section of the arms with the four pockets formed by the fusion of the buccal points with the sail-shaped protective membrane of the dorsal arms.

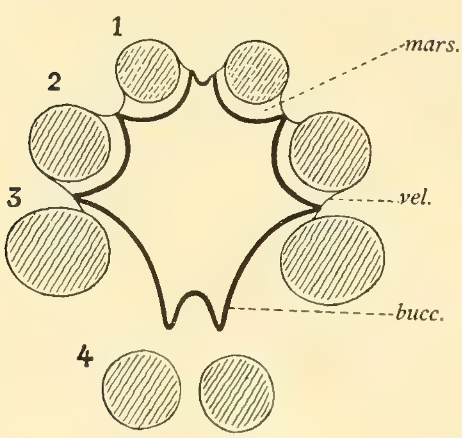

FIGURE 21. Diagrammatic cross section of buccal funnel and bases of arms of *Pterygioteuthis*:

1, 2, 3, 4 1st–4th arms cut; *bucc.* buccal funnel; *mars.* pocket-like spaces; *vel.* sail-like widening of posterior membranes.

Pyroteuthis shows a similar condition, with 4 buccal pockets at the 4 dorsal arms. The attachment between the 2nd and 3rd arms of *Pyroteuthis* is shown in Plate XIII, Figure 6. The 3rd buccal pillar forms a thick attachment to the 3rd arm, while the pillar tapers as it undulates toward the base of the buccal funnel. The sail-like connection between the bases of the arms is so completely fused
114 with the outer side of the buccal funnel that it is indicated only by a projecting fold which extends over a pitlike depression of the buccal membrane.

Pori aquiferi are absent in *Pterygioteuthis* and *Pyroteuthis* because of the fusion between the buccal membrane and the bases of the arms; only two such pores are present on the ventral side of the buccal funnel. This is illustrated in Plate XIII, Figures 1 and 3. In Figure 1, the ventral arms are folded downward after the attachment to the ventral buccal pillars has been cut. The 3rd buccal pillars have a thick attachment (also in *Pyroteuthis*, Figure 6) and taper toward the base of the buccal funnel.

An opening below the 3rd buccal pillar leads into a large sinus between the buccal membrane and the bases of the dorsal arms (Figure 1, *por.*). The spaces between the 3rd and 4th arms and the buccal membrane have to be considered as pori aquiferi. They communicate with each other below the two ventral buccal pillars, as is shown in lateral view of an intact buccal funnel in Figure 3. Between the two ventral buccal pillars and the bases of the arms extends a delicate membrane which forms a pocket with a completely closed floor. This membrane bridges the interval between the two ventral pori aquiferi; the interval is also crossed by the strong, deep attachments extending from the 3rd to the 4th arms.

The young animal in Figure 7 already shows the same condition, i.e., the two pori aquiferi and the two ventral attachments with the pocket which is surrounded by them. These conditions are characteristic for the whole family Enoploteuthidae, although the ventral attachments are displaced upward and the pocketlike depression between them is more distinctly developed.

The deep attachments of the arms of *Pterygioteuthis* are developed as in all Enoploteuthidae. However, it is characteristic for the genus that the attachments between the two 3rd arms form weak, crossing cords to the ventral arms but are fused into a thick muscle which surrounds the basal part of the buccal funnel (Plate VI, Figures 1 and 3); Figure 1 shows also the oblique attachments which extend from the ventral arms to the 3rd pair of arms.

Hectocotylus

A detailed description of the hectocotylization in *Pterygioteuthis* is given because the males of this genus were not known until now.

Pterygioteuthis and *Pyroteuthis* are closely related and it is therefore surprising that these two genera differ so markedly in the hectocotylization. **It affects the right ventral arm in *Pyroteuthis* and**
115 **the left ventral arm in *Pterygioteuthis*.** I thought at first that the statement made by Claus, that the right ventral arm of *Pyroteuthis margaritifera* is hectocotylized, was incorrect. Examination of a well-preserved specimen from Messina showed, however, that this is correct. The right ventral arm bears two rows of hooks which extend along the whole arm and become markedly smaller and more widely spaced where a broad glandular lobe on the ventral side of the distal part of the arm is situated and extends to the inner side, which is covered with suckers (Plate XI, Figures 2, 3). Hectocotylization shows far more primitive conditions in *Pyroteuthis* than in *Pterygioteuthis*, in which the process affects the left ventral arm in both species (Plate XII, Figure 2; Plate XIII, Figure 1; Plate XIV, Figure 1).

Males are more numerous than females in the material obtained by our expedition. All 3 specimens of *Pterygioteuthis giardi* caught were males. The only specimen of *P. giardi* collected by the South Polar Expedition was also a male. My collection of *P. gemmata* contains 2 males and 3 females.

Hectocotylization takes place very early. Only the younger specimens, with a mantle length of less than 7 mm, have both ventral arms uniformly and completely covered with biserial suckers. The youngest male from Station 215 with a mantle length of 8 mm (Plate XII, Figures 3, 4) showed the beginnings of hectocotylization: its right ventral arm bears about 10 pairs of suckers in 2 rows, but not a single sucker on the left arm. This is surprising because the genitalia are very little developed: the testis (Plate XIV, Figure 3) is only 0.8 mm long and is covered by the stomach; only after careful examination did I find the minute male genital duct, which is about 1 mm long and is situated near the branchial heart, far from the testis. A balsam preparation showed that there is already a distinct genital pocket.

A specimen of the same size (Station 218) differs from the above in the absence of suckers on the

right ventral arm. Its left ventral arm bears a high, keel-shaped swimming membrane but no suckers and resembles the definitive condition.

An older male from Station 217 has a completely hectocotylized left ventral arm (Plate XII, Figures 1, 2). The right ventral arm is also without suckers and membranes, except for the keel-shaped swimming membrane.

The oldest and fully mature male of *P. giardi* (Plate XIV, Figure 1) has a well-developed hectocotylus (Plate XV, Figure 1). The right ventral arm shows some characters which are absent in younger stages: it is keeled its whole length by a swimming membrane and bears two knobs which proved to be hooks under the microscope.

Another character connected with hectocotylization in *P. giardi* is the presence of a very large,
116 well developed ventral hook on the 2nd arms of both older males (Plate XIII, Figure 2).

I had no younger specimens of *P. gemmata* and I can only state that the hectocotylus of the mature male (see below) resembles in general that of *P. giardi.* The only distinct difference is the presence of suckers along the whole hectocotylized ventral arm; however, the suckers are smaller than those on the other arms and apparently form a loose uniserial pattern.

The **form of the hectocotylus** (Plate XV, Figures 1–8) is the same in the two species of *Pterygioteuthis*. The left ventral arm has a broad base and tapers in its distal third to a tip which is curved like a hook toward the midline of the body (Plate XIV, Figure 1). There are no suckers, hooks or even a hint of protective membranes. However, the arm bears a large swimming membrane which forms a broad keel from the base to the distal third, where it gradually disappears (Plate XV, Figures 1, 3). The hectocotylus is covered with 2 large pads of glands opposite the swimming margin (Figures 1, 2) which are markedly widened and open near the middle of the arm. In *Pterygioteuthis gemmata*, the distal pad is slightly smaller than the proximal pad. The difference in size is more marked in *P. giardi*, in which the large proximal pad has a reddish color (Figure 1). A very fine striation, visible between the two pads, is caused by radial grooves (Figure 3). In *P. gemmata* these grooves are present on the inner and outer side of the arm, while in *P. giardi* they exist only on the outer surface (Figures 4, 5). The grooved area is here bordered by two conical swellings between which project two large hooks, a smaller proximal and a larger distal hook, both visible from the inner side. These hooks are colorless in younger specimens of *P. giardi* (Figure 5), but they become brown in older specimens (Figure 4). This structure is more complicated in *P. gemmata* because of the presence of a toothed plate that resembles a grate and lies between the two systems of grooves. Examination from the inner side gives a better view of the whole structure (Figure 3).

Information on the nature of this peculiar formation is obtained by sections of the hectocotylus of *P. gemmata* (Figures 6–8). The base of the arm is normal, and the musculature surrounding the thick nerve is covered with a thin outer layer of connective tissue. This changes near the glandular pad, when the connective tissue forms a thick layer in which gland follicles are embedded. A longitudinal section of the distal half of the glandular pad (Figure 6) shows the presence of tubular glands which open in a slightly narrowed opening in the middle of the arm. The beginning of the tubes of the gland is widened and folded. The cross section (Figure 8) shows that there are about 6 gland tubes of different width, which produce a granular secretion.

117 The toothed plate forms a sharp edge in the middle between the two glandular pads (Figure 7); however, it sinks below the gland tubes proximally and distally, and is surrounded by the feltlike connective tissue. A brown, granular pigment is accumulated in the vicinity of the toothed plate (Figure 8). I do not know whether the toothed plate consists of chitin because an epithelial layer which may have produced the plate is absent.

The finely fluted, externally visible system of lamellae is also glandular. The open grooves are lined with gland cells which resemble those of the closed tubes.

The function of this glandular apparatus is not known. However, it is possible that the radial grooves with their lining of gland cells may accommodate single spermatophores.

Mantle Complex (Plate XIV)

A very thin ventral septum connects the **mantle cavity** with the abdominal wall. Opening of the mantle cavity shows the ventral surface of the funnel with its slightly curved posterior end. The two thick depressors of the funnel originate on its dorsal side and extend toward the base of the gills. The **anus**, which is normally covered by the funnel, opens between two lips, on which the spatulate, symmetrical anal appendages are situated laterally (Figure 4).

The **rectum** is completely covered by the ventral abdominal wall which has a golden sheen and also covers the other organs. The openings of the renal sacs are distinct; they form oval papillae (Figure 4, *ur.*). The end of the male gonoduct, the spermatophore sac, situated behind the base of the left gill and the appendage of the prostate situated on the spermatophore sac, are also visible. The **luminous organs** are striking, especially in specimens preserved for a long time in formol in which their sheen is still visible. A detailed description of the luminous organs will be given below. The large, greenish anal organs and the large, flesh-pink organs at the base of the gills are paired. The single abdominal organs have a nacreous sheen. The largest anterior organ is situated at the level of the base of the gills; the 3 posteriod organs end with a small organ situated at the extreme end of the body, which had been overlooked until now.

Male Genitalia (Plate XV)

The male of *Pterygioteuthis*, unknown until now, shows a very early hectocotylization of the left ventral arm. I attempted therefore to obtain more exact information on the genitalia. A detailed description has been given in my earlier publication (1905); only the main points will be mentioned here.

118 The **testis** of the young animal is situated dorsal to the stomach. In the mature male, however, it covers part of the stomach and extends far toward the posterior end of the body. The male gonoduct (Plate XV, Figure 9) begins with the slitlike opening of the vas deferens into the body cavity. It forms irregular undulate curves dorsal to the first part of the seminal vesicle (*ves.sem.1*), after which it extends anteriorly and finally enters the seminal vesicle. The first part of the spermatophore gland, as Marchand (1907) named the seminal vesicle, is large and oblong; it narrows slightly near the smaller middle part (*ves.sem.2*). Ventral examination of this part shows developing spermatophores in the S-shaped gonoduct. The 3rd part is oblong, with smooth walls. It consists of 3 parts, marked α, β, and γ in the figure. The first part is short and thick; the long middle part extends obliquely anteriorly and the narrow terminal part opens in the long, saclike prostate which is longitudinally striated; at the junction with the terminal part of the seminal vesicle, it bears a very long caecum which projects far into the mantle cavity (Plate XIV, Figure 4). The short vas efferens extends along the appendage of the prostate and opens into the spermatophore sac (*b.sperm.*) in about the posterior third. Its folds form a slight spiral and become indistinct toward the opening which projects freely into the mantle cavity near the caecum of the prostate above the base of the left gill. I made sections of the gonoduct to determine the function of these sharply differentiated parts. A detailed histological description will

be given by my student Marchand. Briefly, the first part of the spermatophore gland contains cylindrical and spindle-shaped cells with a secretory vacuole near the nucleus and with one or two refractile spherical granules. These granules enter the gland ducts and fill the sheath of the spermatophore around the tube which contains the spermatozoa. I assume that the granules swell outward while the spermatophore is emptied, and cause the eversion of the sperm tube.

The path of the spermatophore in the gonoduct has already been described in *Abraliopsis*. I will only mention here that, according to the studies of Marchand, the prostate functions as a shunting station which the spermatophores enter with the aboral pole first but leave in the reverse position. I used to believe that this reversal takes place in the long caecum of the prostate, but sections of the caecum of *Pterygioteuthis* showed (Marchand, 1907, p. 27, Figure 5) that this part contains two lumina which are united at the apex. The caecum thus represents the beginning of the vas efferens, which forms a loop with closely approximated arms. A reversal of the spermatophores is thus impossible in this part, which, strictly speaking, is not a caecum at all; it can only take place in the long prostate.

119 Finally, *Pterygioteuthis* also has a long ciliated duct which extends from the terminal part of the seminal vesicle and adheres to the prostate along its whole length. This canal is narrow in the middle and then widens toward the opening. Its epithelium forms longitudinal swellings (Figure 11) and shows distinct cilia in well-preserved specimens which are present to the funnel-shaped terminal part. Similar longitudinal swellings are present in the ciliated funnel, as shown in Figure 10. The ciliated funnel opens in the genital pocket, into which it projects far. Its ciliated epithelium is folded over around the opening and then gradually flattens and passes into the epithelium of the pocket. I could not determine the form of the ciliated cells; the oval, densely packed nuclei, however, are quite distinct.

The physiological function of the ciliated duct and funnel is not known. Brock observed a similar but short duct in *Sepia*; he thinks that the duct serves for the removal of dead spermatozoa. This seems improbable, because Marchand (p. 25) and I never found spermatozoa there. We know only, as Marchand observed in the live animal, that the cilia move toward the genital pocket. As noted earlier (p. 29), this pocket is not a part of the body cavity but an invagination of the outer surface, which is lined with ectoderm and sometimes remains open.

Female Genitalia

As I had only males of *P. giardi*, I shall describe the genitalia of a female *P. gemmata*. The genus *Pterygioteuthis* has nidamental glands, in contrast to *Abralia* and *Abraliopsis*. The specimen examined, which was apparently ready for oviposition, has nidamental glands that are so large that they cover most of the visceral sac. The glands are paired, oblong, 10 mm long and 3 mm wide. They end posteriorly between the 2nd and 3rd ventral luminous organs; their opening projects to the upper third of the gills. The two glands are contiguous in the middle, so that the viscera below them are slightly compressed. Their anterior opening is situated between two lyre-shaped lobes. The opening of the right oviduct with its divergent glands is situated slightly above the opening of the right nidamental gland. A left oviduct apparently is absent; it could not be found even after removal of the left nidamental gland. There is thus apparently only a right oviduct. The condition was similar in another female examined.

120 ## Luminous organs

(Plates XIV, XVI)

The luminous organs of *Pterygioteuthis* and *Pyroteuthis*, especially those of the eyes, were described only superficially in the past. *Pterygioteuthis* has also ventral organs. These were first described in detail by Hoyle for *Pyroteuthis* (1902) and *Pterygioteuthis* (1904, pp. 51–58, Plate IX). These observations certainly gave valuable information, but I am in the position to enlarge upon it. In particular, the polymorphism of the luminous organs is more far-reaching than it appears from Hoyle's description.

Arrangement of the Luminous Organs

The luminous organs of *Pterygioteuthis* can be divided into organs of the eyes and ventral organs. The organs on the eyes are distinct, as they are covered only by a thin lid fold. The ventral organs become visible only after opening of the mantle cavity in preserved specimens, but they shine through the transparent mantle in the live animal (Plate XII). The organs are very variable in size and form: spherical, oval, conical or lens-shaped. Most of them have a radial structure, but the flattened organs, e.g. the large organs at the base of the gills, are bilaterally symmetrical. Specimens preserved in formol show the full sheen of the organs. One can hardly imagine a more magnificent play of colors; they shine on a dark background like pearls and precious stones, the larger organs of the eyes like blue sapphires, the anal organs like greenish or golden metallic mirrors, the organs near the gills with a flesh-pink tone, the others with a nacreous sheen. Transfer of the specimen to alcohol destroys this brilliance; the scalelike superimposed cells and concentrically stratified lamellae shrink, and the greenish metallic sheen becomes steel blue and later disappears.

The eye organs apparently cover the whole ventral surface of the eyeball irregularly. Closer examination shows, however, that the arrangement of these organs is the same in all specimens. Thus, 10 larger organs form a more or less *S*-shaped curve. The 7 organs in the anterior curve are situated closer together than the 3 posterior organs (Plate XIV, Figure 1). In addition to these 10 organs, there are 4
121 small organs in *Pterygioteuthis gemmata* and 5 in *P. giardi* on the ventral inner surface of the eyeball which become visible if the eyeball is slightly turned outward (Figures 5, 6). Because his specimens were damaged, Hoyle could not determine the number of eye organs; he assumed that 5 organs are present on each eyeball. In fact, there are 14 organs in *P. gemmata*, and 15 in *P. giardi*. The larger organs are 0.5–0.8 mm wide, the smaller ones 0.3–0.4 mm.

The ventral organs are divided into anal and branchial organs. The anal organs (siphonal organs of Hoyle) form a pair near the anus. The paired branchial organs are situated at the base of the gills close to the branchial hearts. There are also unpaired abdominal organs. The largest anterior organ is situated at the level of the base of the gills between the branchial organs but slightly more anteriorly. Then follow two smaller organs situated on the posterior end of the body near the end of the gladius. These 4 organs decrease gradually in size posteriorly. Hoyle noticed only two of them and also overlooked the small organ situated on the tip of the gladius of *Pyroteuthis* (Plate XI, Figure 1). The ventral organs differ markedly in size; the oval branchial organs are 1.5–17 mm wide, the conical anal organs 1–1.2 mm, the anterior abdominal organ 0.8 mm, the middle organ 0.5 mm and the posterior only 0.3 mm.

Thus, *P. gemmata* has 36 and *P. giardi* 38 organs.

General Review of the Structure of the Organs (Plate XVI)

The **luminous body** (central mass of HOYLE) is always situated centrally (*phot.*) and is surrounded by various formations such as the pigmented sheath, reflectors and lenses. It may be conical, oval or rounded; the flattened organs have an elongate luminous body. In the branchial organs (Figure 13), the luminous body consists of two separate parts which differ markedly in size. As each of these parts is surrounded by a separate reflector, the organ near the gills is thus double.

The cells which form the luminous body are strictly uniform in all organs, although the organs are of very different form. The cells are most distinct in the large luminous body of the organs near the gills. In general the cells are polyhedral and closely packed, with gaps filled by nerves and blood vessels (Figures 14, 19). They stain only very weakly (acid carmin, hemalum, iron-hematoxylin), except their small, round, rarely oval, nuclei. There is usually a single dark nucleolus and sometimes a larger number of chromatin granules. The cytoplasm is otherwise homogeneous and strongly refractile. In the eye organs, in which the cells are as indistinct as in the anal and abdominal organs, the
122 cytoplasm consists of smaller flakes, mainly in the conical apex of the luminous body.

A **pigmented sheath** surrounds all organs on the inner side. In eye organ No. 6 (Figure 6), the sheath may extend also to the outer side and sometimes surrounds the whole organ. The pigment of the sheath is blackish brown, sometimes lighter brown in the smaller organs of the eye, and is embedded in stellate cells of connective tissue. Chromatophores are never present in the pigmented sheath.

The **squamous cells** (*sq.*) are strongly refractile and were already described for the genus *Thaumatolampas*; they are present in all organs, except eye organ No. 6 and the small organs of the eye. They are present mainly in the reflector, but sometimes also enter the luminous body; they form the lens in some eye organs (Figure 1). The squamous cells usually are layered in concentric layers like roof tiles. They have a peripheral nucleus which is usually oval but may be round or irregularly indented (Figure 16). The strongly refractile cytoplasm is sometimes homogeneous and sometimes consists of numerous concentric layers which may form fibers after preservation. The outline of the cells is irregular, often indented. The squamous cells of the reflector are usually smaller; those which enter the luminous body or form lens-shaped thickenings are often rather large (Figure 12, *l.sq.*). Since the latter cells divide into fibers and form layers of lamellae, this structure probably causes the metallic sheen of the eye and anal organs.

Systems of lamellae (*lam.*) often increase the effect of the reflector. They form a layer (inner cup of HOYLE) between the reflector and the luminous body. If squamous cells are absent, e.g. in the small eye organs, in organ No. 6 and in the large double organ near the gills, the systems of lamellae alone act as reflectors.

The systems of lamellae consist of thin, wide lamellae, covered with flat, oval or irregularly formed cells (Figure 15). Vessels and nerves pass through the lamellae before they reach the luminous body; if they are examined from the surface, the system of lamellae therefore shows numerous sharply delimited holes, filled with small vessels or nerve fibrils. Shrinkage of the lamellae after preservation causes irregular folds which radiate from the holes.

Strands of connective tissue (*fibr.*) take part to a varying extent in the structure of the luminous organs. I never found a distinct envelope of subcutaneous connective tissue around the organs. The luminous body, however, contains strands of connective tissue; in the large eye organs and in the anal organs, these strands surround the squamous cells (Figures 1, 12).

A thick layer formed by a network of thick, connected rods covers the outer surface of the large organs near the gills and also separates the large and the small luminous bodies (Figure 13). A similar

123 system of connective tissue strands forms the outer surface of the lens of the anal organs and passes into a system of concentric lamellae toward the margin (Figure 12, *l. coll.*).

The **lenses** consist of various tissues, including of connective tissue and squamous cells. Two other categories of cells form the lenses of some eye organs and the abdominal organs. Thus, the posterior flattened eye organs, especially organ No. 10 (Plate XIV, Figures 6, 7), bear a complex of polyhedral cells with small, round nuclei; seen from the surface, these cells form a hemispherical lens. The cells are homogeneous except those which are situated near the squamous cells (Plate XVI, Figures 2, 3, *l'*). These cells are filled so uniformly with granules that they can hardly be considered to be the same as the other light cells of the lens. I found such granulate cells not only in the flattened organs but sometimes also as a lateral cluster in the radial eye organs (Figure 1, *l'*).

The fibrous systems which form the lenses in front of the abdominal organs are quite different (Figures 10, 11, *str.*). These lenses consist of fascicles of silky fibers which are situated at the outer margin of the luminous body, separated from it only by an envelope of connective tissue, and radiating toward the convex outer surface of the organ. These fibers have oblong nuclei; at the base, where the fascicles converge, the nuclei are more rounded or oval. A similar fibrous system which possibly also functions as a lens is situated between the large and small luminous bodies of the organs near the gills (Figure 13, *str.*).

The **blood supply** is of particular importance in the luminous organs of *Pterygioteuthis*. The blood vessels usually extend from the inner surface toward the luminous body. The luminous body is regularly surrounded by small vessels which branch and usually pass straight through the reflector and systems of lamellae (Figure 15, *cap.*) and finally form a capillary network inside the luminous body. The course of the capillaries can be followed by the oblong, oval nuclei, which are sometimes arranged in rows, particularly in the large luminous body of the organs near the gills. The vessels pass through gaps between the luminous cells, without entering the cells.

The **nerves** also pass radially through the reflector and systems of lamellae (Figure 15) and then branch near the luminous body and form fibers with oblong, finely granulate nuclei. After many unsuccessful attempts to stain the nerve fibrils, I finally succeeded in staining the eye organ with iron-hematoxylin after fixation with sublimate. The fibers stain deep black, in contrast to the surrounding light-colored tissue, giving a clear picture of the innervation of the luminous body. Figure 17 shows
124 the course of 3 fibers which pass through the concentric system of lamellae and the connective tissue; after a slightly undulate course, they divide into very thin branches which disappear between the luminous cells. At other points there were 2 or 3 adjacent fibers, deeply stained to the terminal branches (Figure 18). As each section shows several fibers entering the luminous body, the nerve supply is apparently very rich. The same applies to the lamellae, which are densely crossed with numerous nerves (Figure 15).

Polymorphism of the Luminous Organs

The organs of *Pterygioteuthis* are nearly as polymorphic as in *Thaumatolampas*. The eye organs of *Pterygioteuthis* form 4 structural types, only one of which has been described previously—by myself (1903), and by Hoyle (1904). The organs near the gills, the anal and the ventral organs are also markedly different. It is therefore in order to describe the structure of each type of the various organs.

1. Large Anterior Organs of the Eyes
(Plate XVI, Figures 1, 15, 17)

These organs are numbered 1 to 5 in the figures. Figure 1 shows a typical, well-preserved organ of *P. gemmata* preserved in formol. This is organ No. 1 in Plate XIV, i.e. the anterior of the large organs of the eyes. It is radially ovoid. In the center is the conical luminous body (central mass of Hoyle), bordered anteriorly by the lens, laterally by the system of lamellae and posteriorly by the reflector. The anterior half of the luminous body bears a single layer of large, strongly refractile squamous cells (*sq. int.*), which are separated by fine strands of connective tissue which branch between the luminous cells. The reflector consists of two distinct formations: a. fine systems of lamellae (*lam.*) which extend from the conical apex of the luminous body to the lens, forming a thick envelope which widens anteriorly (inner cup of Hoyle); b. squamous cells (*refl.*) in dense, multiple layers, particularly around the rounded-conical apex of the luminous body, and extending to the systems of lamellae (posterior cup of Hoyle). A dense, reddish brown pigment (capsule of Hoyle) in the ramified cells of connective tissue surrounds the organ to the margin of the lens. An envelope of connective tissue is absent, although the numerous vessels and nerves cause some thickening of the tissue. The vessels form a radial pattern, passing almost straight through the reflector and then through the systems of lamellae (Figure 15). The same applies to the nerves, the branching of which has been described above (Figure 17).

A convex lens is situated in front of the luminous body. A thin layer of connective tissue separates the lens from the luminous body and the systems of lamellae. The lens consists of large squamous
125 cells, surrounded by strands of connective tissue which extend from the fibrous layer of connective tissue situated before the luminous body and the system of lamellae (*fibr.*).

The lens of some organs contains lateral clusters of granulate cells (*l'*) which resemble the inner cells of the lens of some eye organs.

Hoyle (1904, p. 52, Figure 2) described and illustrated the radial eye organs of *P. giardi*. Despite the unsatisfactory preservation of his material, as shown by the drawing, he distinguished the main components of the organ. I found formol the best preservative for the luminous organs. Sublimate and Müller's fluid proved less satisfactory but staining with iron-hematoxylin showed perfectly the nerves which enter the luminous body in a specimen fixed with sublimate. The luminous cells of organs fixed with sublimate are not homogeneous but very finely granulate. The systems of lamellae and the squamous cells stain intensively blackish blue with iron-hematoxylin, while the luminous body and the connective tissue remain pale.

2. Flattened Organs of the Eyes
(Plate XIV, Figure 7; Plate XVI, Figures 2, 3, 4)

The radial organs of the eye closely resemble the flattened organs; the difference between the two types is caused mainly by their bilateral symmetry. Especially characteristic for the flattened organs is the large lens; it consists of cells which are present only in traces in the radial organs.

Figures 2 and 3 of Plate XVI show the effect of the flattening. In the median section, the reflector extends along a large part of the lower surface, i.e., the side facing the eyeball; on the outer surface it ends broadly truncate. The systems of lamellae (*lam.*) are also affected by extreme flattening (Figure 3): they become long on the lower side and are shortened on the outer side. Figure 3 shows that the

luminous body also extends obliquely toward the lower side, while the outer squamous cells, which form a lens (*l'*), form only a thin layer.

Because of the flattening, the squamous cells of the reflector which surround the apex of the luminous body appear sickle-shaped (*refl.*). All structural elements of the radial organs are thus present. This is shown (Figure 3) of organ No. 10 of a young specimen of *P. giardi.* The squamous
126 cells in the luminous body are also present and so are the densely granulate cells (*l'*) situated in front of the outer squamous cells which form a lens. The whole organ is surrounded by a pigmented sheath which is thick at the apex of the reflector; it becomes thinner toward the lower side and even extends to the outer surface.

Comparison of this organ with the corresponding organ (No. 10) of *P. gemmata* (Figure 2) shows that it differs from it mainly in the presence of a large lens (Plate XIV, Figure 7). The organ is not so markedly flattened as the organ described above, but it permits a clear homology with the components shown in Figure 1. The lens consists of two distinct layers: the concentrically stratified outer squamous cells and large, polyhedral cells with small spherical nuclei. The outer cells of the lens are homogeneous (*l''*), while those adjacent to the squamous cells (*l'*) have a densely granulate content and apparently correspond to the cells described in connection with organ No. 1 and the markedly flattened organ No. 10 (Figure 3). The pigmented sheath of these organs is well developed around the reflector but becomes thinner and disappears toward the lens. Figure 4 shows the same organ of another specimen at lower magnification to demonstrate its position on the eyeball. Of particular interest is the thick layer of fibrous lamellae of connective tissue (*aur.*). This layer is present in front of the lens as a modified part of the outer layer of the eyeball. These loosely arranged lamellae resemble the system of lamellae of the inner layer of the reflector; they cause the golden sheen of the body between the organs and at other points. These layers also stain intensively black with iron-hematoxylin, which proves their relationship to the systems of lamellae of the luminous organs.

3. Large Eye Organ No. 6
(Plate XVI, Figures 5, 6, 7)

Surprisingly, organ No. 6 (counting posteriorly) differs distinctly in structure from the organs described above. This organ may not be visible from the outside but it has a soft sheen in other cases. This is caused by movement of the pigmented layer, which may cover the whole outer surface of the organ or leave it exposed. There is no other explanation for the different illustrations, which show the organ either completely covered with pigment (Plate XVI, Figure 6) or exposed to a varying extent (Figures 5 and 7).

A spherical or oval, or slightly irregular luminous body without squamous cells is situated at the center of the organ. Squamous cells are absent in the entire organ. The reflector (*refl.*) consists only of systems of lamellae, which form a very thick layer. They continue toward the outside into a system of fibers and lamellae of connective tissue which may form a thin (Figure 7) or a thicker layer (Figure 5). The organ is completely embedded in the outer layer of the eyeball, which consists of pigmented,
127 ramified cells of connective tissue around the reflector. Figure 5, in which the outer layer of the eyeball which covers the organ is torn, shows also the numerous blood vessels (*v.*) near the lower surface which pass straight through the thick reflector. As the pigment sometimes covers the outer surface of the organ, it probably functions as a filter which gives a certain color to the emitted light.

4. Small Organs of the Eyes
(Plate XVI, Figures 8, 9)

The small organs of the eyes, of which there are 4 on the anterior inner surface of the eyeball in *P. gemmata* and 5 in *P. giardi*, extending from the large organ No. 8 (Plate XVI, Figures 5, 6), have never been described. These organs generally resemble organ No. 6 and are a reduced copy of it. They too are surrounded by a thick reflector which envelops a small, ovoid or rounded luminous body (Plate XVI, Figures 8, 9). The reflector also consists of thin, concentrically stratified systems of lamellae which are crossed radially with vessels and nerves. On the other hand, the outer surface of the luminous body of the small organs is covered by a very thin layer of connective tissue. This applies only to the smallest organs; in the largest of these 4 or 5 organs (organ No. 11), there is a lens-shaped thickening with small nuclei but no distinct cell boundaries in front of the luminous body (Figure 8, *l.*). Between this convex lens and the luminous body is a layer of small spindle-shaped cells (*sq.*) which stain intensively and resemble the squamous cells situated in front of the luminous body of the large eye organs. We therefore consider the small organs of the eyes as a separate category which differs from organ No. 6. The pigment of the small organs is situated in ramified cells of connective tissue which are scattered on the lower surface. Between the cells and the reflector is a tissue which passes gradually into the reflector; it resembles in its loose structure and undulate lamellae the tissue which causes the golden sheen of the eyeball.

5. Anal Organs
(Plate XIV, Figure 9; Plate XVI, Figure 12)

The anal organs closely resemble in structure the large organs of the eyes but they differ from them in their smaller size and in the complicated structure of the lens which covers the **luminous body**. The anal organs are acorn-shaped, with slightly convex outer surface and hemispherical inner surface. In the center is the conical luminous body, the rounded apex of which projects toward the reflector. The luminous body contains large, flat squamous cells near the lens (Figure 12, *sq. int.*), with connective tissue between them.

The **reflector** consists of a thick peripheral capsule of numerous concentrically stratified squamous cells and of an inner mantle which is broader toward the lens and consists of thin systems of lamellae
128 (*lam.*). Distinct nerves and vessels pass radially through the reflector. The reflector is bordered posteriorly by a thick layer of pigment which extends to the ventral surface of the lens. Between the lens and the luminous body is a very thick layer of connective tissue (*fibr.*) which also delimits the anterior part of the reflector.

The large **lens** consists of two different layers. The inner layer consists of very large squamous cells (*l. sq.*) the darkly stained content of which consists of concentric lamellae. From the underlying layer of connective tissue extend fibers which surround the squamous cells. The outer layer is very thick and consists mainly of a network of bars of connective tissue (*l.*) which pass in the center into a homogeneous, weakly stained tissue. At the periphery, the connective tissue forms a modified radial pattern of lamellae which Hoyle named "collar" (*coll.*). There is also a fibrous tissue on the inner surface of the lens which closely resembles the systems of the lamellae of the inner layer of the reflector (*lam. l.*).

All these layers of connective tissue are completely transparent in the live animal, while the metallic sheen is certainly caused by the deeper layer of squamous cells.

Hoyle's description of the anal organ is correct in general; it was better preserved than the organs of the eyes, to judge from the drawing.

6. Organs Near the Gills
(Plate XVI, Figure 13)

The organs near the gills have a special position among the organs of *Pterygioteuthis* because they are double, consisting of a large and a small organ. They are also the largest organs, nearly 2 mm wide.

The main mass of the organs near the gills is formed by a large **luminous body** which is divided into two parts: the larger part extends toward the middle of the body, the smaller part faces the gill. The boundaries of the polyhedral cells are more distinct in the large luminous body than in the other organs. The small luminous body (*phot.'*) is surrounded on the side of the gill by a thick layer of squamous cells which form a reflector. Adjacent are large systems of lamellae, of which the system situated on the lower surface (*lam. int.*) is large and envelops the large luminous body. The outer system of lamellae (*lam. ext.*) is thick but short and extends to the outer skin of the organ. A pigmented mantle is present only on the surface which faces the gills; it extends from there along the systems of lamellae. This large reflector, which consists of squamous cells and lamellae, is crossed by vessels and nerves extending from a vascular network (*v.*) which is very dense on the whole lower surface, especially toward the gills.

129 The large and the small luminous bodies are separated by a thick layer of connective tissue (*fibr.*) which becomes gradually thinner and covers the large luminous body from the outside. This connective tissue, too, consists of a network of bars, resembling that present in the lens of the anal organs. The organ has a relatively small **lens** which is situated at the level of the small luminous body between the reflector and the bars of connective tissue and consists of fine, silky fibers (*str.*) similar to those in the abdominal organs.

Between the luminous body and its thick outer cover of connective tissue is a layer (*n.'*) with numerous nuclei from which extend long strands of fibers into the luminous body. These fibers, which have oval nuclei, may safely be interpreted as nerves, because they show a finely fibrillar striation (Figure 19, *n.*). Even the granulate substance observed in the sections at various points in the spaces between the luminous cells (Figure 14, *n.*) may only be the result of cross-sectioning these fibrous strands.

I did not find ganglion cells in the granulate peripheral layer from which the nerves extend. This layer may be comparable to the nervous layer which is situated on the luminous body of the anal organs of *Thaumatolampas* (Plate IV, Figure 14).

Finally, it may be stressed that the outer abdominal wall covers the organ and the cross sections therefore show longitudinal muscles (*mu. l.*) which, however, are absent in the area of the lens and become visible again near the gill.

Hoyle's description of the organs near the gills is apparently based on a badly preserved specimen. He notes that the luminous body is divided into two parts but did not recognize that it is a double organ. Moreover, several structures mentioned here escaped his attention.

7. Abdominal Organs
(Plate XVI, Figures 10, 11)

The abdominal organs decrease in size posteriorly. I made sections of the anterior and the following organ; there is apparently no distinct difference between them.

The anterior abdominal organ (Plate XIV, Figure 4) is oval, 1 mm wide and surrounded by a pigmented ring. Internally it also has a radial structure. The conical luminous body is situated in the center (Figure 10, *phot.*) and is covered with a thin layer of connective tissue. The luminous body is surrounded posteriorly by a reflector which consists of an inner layer of lamellae (*lam.*) and a dish-shaped outer layer of squamous cells. Vessels and nerves enter the two layers at some points.

The tissue which we have to consider as a lens is very characteristic. It consists of very fine fibers (*str.*) which originate in fascicles from the anterior margin of the luminous body or from the layer of
130 connective tissue and diverge radially toward the periphery. The nuclei at the base are of irregular or oval form, and the peripheral nuclei are oblong. The system of fibers causes the silky sheen, which is also characteristic for all other abdominal organs. The system of fibers is surrounded posteriorly by a thick, brownish black layer of pigment which extends to the margin of the fibers of the lens. A thin outer membrane (*cps.*) covers the organ; the cutis is not dense around the organ, but it contains numerous vessels (*v.*) from which extend the branches that enter the organ.

The following organ (Figure 11) differs distinctly from that described above in its bilaterally symmetrical structure. However, this causes only slight modifications, so that the organ cannot be considered as a new type. Its luminous body is spherical and, again, surrounded by a thick reflector which consists of two layers. The pigment extends to the posterior outer surface of the organ where it becomes very thick. The characteristic system of fine fibers in the lens is present in this organ as well.

Pterygioteuthis has thus at least 7 categories of luminous organs, some of which are similar while others are distinctly different. Only the luminous body with the entering nerves and vessels shows the same structure in all organs. If we assume that the light emitted by all the organs is equal in quality and differs only in intensity, depending on the size of the luminous body, it still must become markedly modified by the accessory structures around the luminous body. The organs have different colors not only in the live animal but also after preservation with formol. The iridescent metallic sheen of the eye and anal organs is probably mainly caused by the effect of thin lamellae which are formed by squamous cells. However, it is not known to what extent these lamellae modify the light from the luminous body. It is also not known whether the systems of fibers of the abdominal organs and the thick layer of connective tissue which forms a lens in front of the luminous body of the anal organs change the quality of the light. However, it is certain that the color of the light is different when a more or less thick layer of pigment is situated on the luminous organ. This applies especially to eye organ No. 6, but also to other eye organs the lens of which is covered to a varying extent by an apparently contractile layer of pigment.

This marked polymorphism of the eye organs of *Pterygioteuthis* is absolutely and relatively less developed than in *Thaumatolampas*, in which the 22 luminous organs show 10 different structural principles.

Measurements of the larger mature male of *Pterygioteuthis giardi*

Total length (without tentacles)	26 mm
Dorsal length of mantle	17 mm
Width of head	9 mm
Largest width of mantle	8 mm
Width of a fin	5 mm
Length of dorsal base of fin	2.3 mm
Length of 1st arm	5.3 mm
Length of 2nd arm	6 mm
Length of 3rd arm	8 mm
Length of 4th arm	7 mm

Postembryonic development of *Pterygioteuthis*

(Plates XII, XIII, Figures 9–12)

I was able to follow the postembryonic development of *Pterygioteuthis* in a complete series, down to the freshly hatched larva. I will begin the description with the oldest and end with the youngest stages. If the reverse method were used, which is obviously more natural, it could not be demonstrated that the youngest stages do in fact belong to this genus, because of their markedly aberrant form.

I begin, therefore, with an older stage which undoubtedly belongs to *Pterygioteuthis*. It was caught at Station 117, in a southern branch of the warm Agulhas Current. Its measurements are as follows:

Total length	9 mm
Dorsal length of mantle	6 mm
Width of head at level of eyes	4.2 mm
Width of a fin	2 mm

The characteristic form of this specimen (Plate XII, Figure 5) closely resembles a smaller adult specimen of *Pterygioteuthis*. The tentacles are relatively short, not longer than the 3rd arms, but the posterior end of the body forms the characteristic pointed tip which projects only slightly beyond the fins.

The arm formula is 3, 2, 1, 4 (the 3rd, 2nd, and 1st arms are 2.8, 2.5 and 2 mm long, respectively). The adult animal has the same formula. All arms bear small suckers, which are also present on the ventral arms, but in a nearly uniserial pattern of about 9–10 suckers. The suckers are more numerous on
132 the other arms; the 3rd arms bear 11 pairs of suckers which decrease in size toward the tip. The swimming membranes are wide on the 3rd arms, smaller on the 2nd arms and only weakly developed on the other arms.

The **tentacles** show the characteristic lyre-shaped bend at the base and the two spindle-shaped basal widenings. A thin membrane fills in the lyre-shaped bend. The club is hardly defined from the tentacle; it is very short and bears dense, small suckers which gradually decrease in size toward the tip. There is a larger proximal sucker, followed by 3 further suckers and about 13 dense quadriserial rows of suckers. The tip of the club is curved back, so that it is difficult to count the suckers.

The other conditions resemble those in the adult animal but the fins are relatively smaller. The arrangement and number of luminous organs show only minor differences; the eye organs are well developed and there are 9 larger organs and two small organs on the inner margin of the eye. The

anal organs and the organs near the gills are visible through the delicate gelatinous mantle on the ventral side.

A similar gelatinous consistency is also present in the stage shown in Figure 6. This specimen, caught at Station 66 in a southern branch of the Guinea Current, is of about the same size as that in Figure 5: it is 9 mm long and its dorsal mantle length is 5 mm. It has a pointed posterior end which projects beyond the fins, which are relatively smaller, only 1.2 mm wide. The ventral arms are long; the tentacles are lost. This stage resembles the adult still more closely than the specimen described before, because of its slender body.

The young stages described below differ from the older stages in their blunt posterior end which does not project beyond the fins.

This applies particularly to the specimen in Figure 7, from the South Equatorial Current. Measurements: total length 6 mm, length of mantle 3 mm, width of head at level of eyes 3 mm, largest width of mantle 2.3 mm.

This stage has a plumper body than those described above. It may appear doubtful whether it belongs to *Pterygioteuthis*, because of the rounded posterior end and the two small fins (their transverse width is about the same as that of the head); their dorsal bases diverge widely and end at the level of the rounded tip of the gladius. However, the arrangement of the luminous organs shows clearly that the larva belongs to the developmental cycle of the pterygiomorph Enoploteuthidae. Each eye bears 9 organs of which Nos. 2, 3, 4, 5 and 7 (see above) have distinct pigmented cups, and the
133 other 4, Nos. 1, 6, 8 and 9, appear only as whitish dots. The anal organs also have pigmented cups, which are visible through the mantle near the ink sac. Since this arrangement and the number of the organs are special characters of the Pterygiomorphae, there is no doubt about the identity. The tentacle also shows the two characteristic thickenings and a bend in the basal part, although the tip is lost. The arm formula is 3, 2, 1, 4, although the 2nd and 3rd arms are almost of equal length. The olfactory tubercles are well developed on each side of the funnel below the eyes.

Figure 8 shows a slightly younger stage from the South Atlantic, with a length of 5 mm, a dorsal mantle length of 2.7 mm and a width of the head of 2.7 mm. As the figure and measurements show, the body is even plumper than in the previously described stage. The arms are relatively short and differ only little in length. The formula is also 3, 2, 1, 4. The ventral arms are very short but their base can be followed to the middle of the head. Next to them are the tentacles, with two spindle-shaped swellings at the base; the clubs are lost. The fins are smaller than in the stage described before; they diverge more strongly dorsally. The dorsal muscular plates of the mantle also diverge widely, so that the posteriorly rounded gladius is visible. The eyes bear 6 luminous organs at the posterior end which correspond to Nos. 2, 3, 4, 5, 7 and 9.

We have a well-preserved specimen of a slightly younger stage from the Atlantic South Equatorial Current. This specimen, shown from 3 sides in Figures 9, 10 and 11, is 4.7 mm long. The width of the head, measured across the protruding lenses, is 2.5 mm, and the dorsal length of the mantle is 3 mm.

The short arms show the same proportions as in the previously described stages. The tentacles are contracted but show the characteristic *S*-shaped bend in lateral view (Figure 11). The ventral view shows that the thick proximal part is distinctly differentiated from the distal part. The small fins project beyond the rounded posterior end of the body; they are attached at the margin of the broadly diverging muscular plates of the mantle (Figure 9). Despite the small size of the larva, the eyes already bear 7 distinct organs which correspond to Nos. 2, 3, 4, 5, 7, 8 and 9; most of the organs (2, 3, 4, 5, 7) have pigmented cups. The anal organs are also slightly pigmented, and are visible through the mantle near the ink sac. This specimen is strongly pigmented and already shows the symmetrical arrangement

of the chromatophores described by JOUBIN for juvenile stages of Cephalopoda. The 1st, 2nd and 3rd arms each bear one chromatophore. There are 6 chromatophores on the dorsal side of the head (Figure
134 9): 2 median, the other 4 lateral. There are 3 further pairs of chromatophores laterally behind the eyes. The dorsal side of the mantle bears a pair of particularly large chromatophores, behind which are 3 further pairs, some of them situated directly in front of the fins. There are 3 chromatophores at the posterior end of the body on the ventral side (Figure 10).

Another specimen of about the same stage (Figure 12) has extended tentacles which show clearly the characteristic bend at the base in lateral view. This specimen from the Indian Countercurrent (Station 231) is about as large as the former specimen and has the same luminous organs and the same arm formula. The extended tentacle permitted closer examination of the club, which differs from that shown in Figure 5 only in the less numerous groups of quadriserial suckers which follow several groups of biserial and triserial suckers (Plate XIII, Figure 11).

The stages between those described above and the youngest larvae are of interest. I have 4 larvae which are shown in Figure 13, with a dorsal mantle length of not more than 2 mm. They have a rounded posterior end. Their fins are very small and widely separated. The arms are short and stump-shaped and the ventral arms are much shorter than the others. In some of them, the 3rd arms are slightly more developed than the 2nd and 1st arms; there is almost no difference in the others. One of the larvae has two small, stalked suckers on each of all 8 arms, while more numerous paired suckers are present on the arms of another specimen of the same size. All suckers become smaller distally; the 1st, 2nd and 3rd arms of this specimen bear 6, 5 and about 6 pairs of suckers respectivelv. There are no suckers on the ventral arms. The tentacles show the characteristic *S*-shaped proximal curvature, but the double swelling is hardly indicated.

Of particular interest is the form of the club, which resembles the most primitive condition. It bears only 7 small stalked suckers, one of them proximal, the others forming 3 pairs (Plate XIII, Figure 12). In two cases there were 7 suckers on the left club but only 5 on the right club. The specimens of this group differ markedly from each other in the development of the luminous organs. One specimen, which is only a little larger than the others, has 5 organs on each eye. Another has only one organ, which apparently corresponds to No. 8 and already has a pigmented cup. The chromatophores are either absent or contracted to small dots. The eyes are relatively large and oval.

The youngest stage (Figures 14, 15) has a similar characteristic form. Figure 14, drawn to the same
135 scale as the preceding figures, illustrates its resemblance to the older stage in Figure 13 in the general form of the body. This stage, of which I have a number of specimens from the Indian North Equatorial Current (Station 214), is only 2 mm long and has a mantle length of 1 mm. The 3rd and 4th arms are much smaller than the 1st and 2nd arms. As the 2nd arms are slightly larger than the 1st, the formula is 2, 1, 3, 4. Each of the 1st and 2nd arms bears 2 small suckers; none are present on the stumpy other arms. The tentacles show the distinct bend at the base and already have a fine membrane in the angle. The club (Plate XIII, Figure 9) bears only 5 suckers, one of which is proximal, the other 4 crown the tip of the tentacle. The same number of suckers is present on the club of slightly older stages. The eyes are relatively large, oval and situated on the strongly protruding optical ganglion. Luminous organs are absent. The posterior end of the body is shown in Plate XIII, Figure 10. The muscular plates of the mantle diverge widely, showing the transparent gladius with rounded posterior end. The caecum of the stomach is visible beneath the gladius. The small, spatulate fins are widely separated because they are attached on the posterior lateral margin of the muscular plates.

That this larva, which is apparently freshly hatched, certainly belongs to *Pterygioteuthis* seems to be quite obvious, in view of its marked resemblance to the slightly older stages in the above-

mentioned characteristic bend of the base of the tentacles, the form of the club, the large transverse eyes and the characteristic form of the posterior end.

The postembryonic development of *Pterygioteuthis* shows that some of the special characters of the Pterygiomorphae appear only at a very late stage. This applies particularly to the projection of the posterior end of the body beyond the fins and the formation of hooks on the arms. On the other hand, the basal bend and the double swelling of the tentacles appear very early, so that there is no doubt about the systematic position of the youngest larvae, especially as this condition does not occur in the Enoplomorphae. Another distinctive character is the arrangement of the luminous organs; around the eye the arrangement of the organs develops early, which is characteristic for the Pterygiomorphae. It is not surprising that some organs develop before the others; the largest of the eye organs (No. 8) appears first. The younger stages differ so strikingly from the adults that their determination would be nearly impossible without the characters of the luminous organs and tentacles. Particularly characteristic
136 for the young stages are the plump body, the rounded posterior end and the wide separation of the fins.

The description of the postembryonic development of *Pterygioteuthis* demonstrates the need for care in the use of relative characters for the determination of species and genera.

Pyroteuthis Hoyle, 1904

Pyroteuthis margaritifera Rüppell

(Plate XI, Figures 1–4)

Enoploteuthis margaritifera Rüppell, 1884, p. 129, Figure 1.
Enoploteuthis margaritifera Gray, 1849, p. 48.
Enoploteuthis margaritifera Vérany, 1851, p. 82, Plate 30, Figure a.
Enoploteuthis margaritifera Claus, 1858, p. 262, Plate X, Figures 2, 2′, 2″.
Enoploteuthis margaritifera Hoyle, 1886, pp. 37, 171, Plate XXIX, Figure 11.
Enoploteuthis margaritifera Joubin, 1894, p. 62.
Enoploteuthis margaritifera Ficalbi, 1899, p. 79 (reprint of the original description of Rüppell).
Pterygioteuthis margaritifera Pfeffer, 1900, p. 166.
Pterygioteuthis margaritifera Hoyle, 1902, p. 42, Figures 1–6.
Enoploteuthis margaritifera Lo Bianco, 1903, p. 170, Plate VIII, Figure 21.
Pyroteuthis margaritifera Hoyle, 1904, p. 42.
Pyroteuthis juv. Issel, 1908, p. 213, Plate IX, Figures 22, 23.

Enoploteuthis margaritifera was discovered in 1844 in Messina by Rüppell, who described it in a letter to Professor Cocco accompanied by a rather crude drawing. The letter was published in the little-known *Giornale del Gabinetto letterario di Messina* (Volume V, 1844, pp. 129–135), and the original publication was therefore copied by Ficalbi (1899). The original drawings by Rüppell are kept at the Senckenberg Library in Frankfurt a.M. Examination of these drawings shows that Rüppell made two drawings of *P. margaritifera.* The published drawing unfortunately shows the characteristic form rather unsatisfactorily. The second drawing, with the name *Veranya margaritifera* (p. 49), is so correct that it has not been surpassed. The drawing of the club is better than that of Vérany, who copied the form (Plate 30, Figure a) too closely from the drawing Rüppell sent to Cocco. In particular, the large eyes, the very wide head, the rounded fins and the strong arms are shown less correctly than in the second drawing of Rüppell.

Some morphological characters of *Pyroteuthis* have already been mentioned in connection with
137 the description of *Pterygioteuthis*, but it is advisable to describe some characters in greater detail and to mention a number of details which have been overlooked.

Hoyle proposed the new name *Pyroteuthis* for *Enoploteuthis margaritifera* because the ventral arms, the tentacle clubs and the luminous organs differ from those of *Pterygioteuthis*. However, the equipment of the ventral arms with hooks and suckers varies widely in both species of *Pterygioteuthis*, and Hoyle apparently overlooked some luminous organs in *Pyroteuthis*. This leaves only the differences in the form of the hand part of the tentacle club—sufficient for the establishment of a new species but not for the establishment of a new genus. I was therefore at first reluctant to accept the new genus *Pyroteuthis*, until I found that hectocotylization affects the left ventral arm of *Pterygioteuthis* and the right ventral arm of *Pyroteuthis*.

Pfeffer (p. 164), like Jatta, states that the ends of the 2nd, 3rd and 4th arms are bare. After examination of the arms of a well-preserved female from Messina, I can give the following details. The 1st arms bear 12 pairs of hooks and 10–12 pairs of densely arranged suckers at the distal end, which decrease gradually in size toward the tip. The 2nd arms have 2 pairs of suckers at the base, followed by 9 pairs of hooks and 2 pairs of tiny suckers at the tip. The 3rd arms have 9 and 10 pairs of hooks and 2 pairs of tiny suckers at the tip. The right ventral arm bears 14 pairs of hooks and 7 pairs of small, widely separated suckers. As the left ventral arm also shows 7 pairs of loosely arranged suckers in the distal part, it is clear that the presence of suckers at the tips of the arms is typical and that their number is greatest on the 1st and 4th arms.

Jatta (p. 88) stated that only the 3rd arms have a swimming membrane, but I found this also on the 1st and 2nd arms, although the membranes are much more weakly developed than on the 3rd arms and are present only in the distal half.

The first arms of my male are very short and end in a finger-shaped process. They have only 5 pairs of hooks which increase in size toward the tip. This is apparently the beginning regeneration of an injury, especially since the left 3rd arm is also shortened and bears a finger-shaped stump.

Pfeffer states in his exact description of the **tentacles**: "the ventral median row of the hand part of the tentacle is transformed into a small group of hooks, the dorsal median row and the dorsal marginal row apparently form together a single broken line of larger suckers, the ventral marginal row consists of small suckers."

This description agrees with the condition in the female (Plate XI, Figure 4). The carpal part is formed by 3 suckers between which are indistinct knobs formed by the impression of the opposite
138 suckers. Then follows the hand part, with a weakly developed protective membrane and with 5 hooks transformed from suckers of the ventral median row; the ventral suckers are very small, and the dorsal rows of suckers are almost uniserial; an alternation of the dorsal suckers is more distinct on the right tentacle.

The **buccal funnel** shows the complicated conditions described for *Pterygioteuthis*. The two dorsal pillars of the funnel of *Pyroteuthis* are situated close together and are almost fused. The attachments extend dorsally from the pillars to the 1st, 2nd and 4th arms, ventrally to the 3rd arms. The pillars taper toward the base of the buccal funnel, where they reach the arms. A thin membrane extends between the thick ventral attachment and the thin ventral pillars. Around the base of the buccal funnel extends a circular sinus which opens to the outside between the 3rd and 4th arms; it is closed by a delicate membrane between the buccal pillars, the inner bases of the arms and the buccal skin.

The **hectocotylization**, which was correctly described by Claus, affects the right ventral arm, which is thick, with a slender tip and bears only hooks. The hooks are bordered in the proximal part

by narrow protective membranes; they are covered distally by a wide ventral lobe of apparently glandular structure. The end of the arm is normal and bears hooks which become gradually smaller toward the tip. My specimen has 10 hooks in the dorsal row and 8 in the ventral row proximal to the lobe. Only 3 small, uniserial hooks are present at the position of the lobe; these are followed distally by 8 alternating hooks of decreasing size. Suckers are absent even at the tip.

The left ventral arm of the male is normal, with 20 pairs of hooks which decrease in size toward the tip.

The **luminous organs** of *P. margaritifera* have been described in detail by Hoyle (1902), who also examined sections. However, Hoyle apparently overlooked some organs.

The **organs of the eyes** form a more or less *S*-shaped curve. Hoyle mentions 9 organs. There are, however, 3 additional small organs on the inner side of the eyeball (Plate XIV, Figure 8). These closely resemble the 4 or 5 small organs of *Pterygioteuthis*.

There are also ventral organs inside the mantle cavity (Plate XI, Figure 1). Hoyle described the position of these organs correctly; there are 2 anal organs, 2 organs near the gills and a number of abdominal organs. The anterior abdominal organs form a row of 3 organs, followed by 2 organs at the level of the base of the fins and a single organ at the posterior end which was overlooked by Hoyle; it corresponds to an organ in the same position in *Pterygioteuthis*.

139 # 2. Family **Veranyidae** Chun

Octopodoteuthis Rüppell

(Plate XVII)

Octopodoteuthis sicula Rüpell, 1844, p. 135 (fide Ficalbi).
Octopodoteuthis Krohn, 1845, p. 47, Plate V, Figures A–F.
Verania sicula Krohn, 1847, p. 39, Plate II, Figures D, E.
Octopodoteuthis sicula Gray, 1849, p. 51.
Verania sicula Vérany, 1851, p. 86, Plate 28.
Octopodoteuthis sicula Pfeffer, 1884, p. 28.
Verania sicula Hoyle, 1886, p. 38.
Verania sicula Weiss, 1889, p. 87, Plate VIII, Figures 1–3.
Verania sicula Appellöf, 1889, p. 6, Figures 12–23.
Verania sicula Jatta, 1896, p. 92, Plate VII, Figure 14; Plate XIII, Figures 1–12.
Octopodoteuthis sicula Pfeffer, 1900, pp. 164, 166.
Octopodoteuthis sicula Massy, 1907, p. 381.
Octopodoteuthis sicula Pfeffer, 1908, p. 74.
Octopodoteuthis sicula Massy, 1909, (I, 1907), p. 28.

The genus *Octopodoteuthis* (*Veranya*) was known until now only from the Mediterranean; our expedition found it also in the Indian Ocean, and Massy (1907, 1909) described it from the Atlantic. It also occurs in the Pacific Ocean: I found an *Octopodoteuthis* in the material collected by Doflein in Sagami Bay, Japan, which closely resembles the Mediterranean *O. sicula*. No distinct specific differences from the Mediterranean form could be found because the specimen is young, with a dorsal mantle length of 15 mm, and had already discarded the tentacles.

The genus was discovered almost at the same time in 1844 by Krohn and Rüppell in Messina. The authors named it *Octopodoteuthis* because of the absence of tentacles. However, Krohn (1847) saw young specimens with small tentacles and proposed the name *Veranya* because the name *Octopodoteuthis* was not correct. This genus was later described as *Veranya* in greater detail by Vérany, who also gave good drawings. The original drawings by Rüppell (kept at the Senckenberg Library in Frankfurt a.M.) have not been published; they are labeled *Octopodoteuthis sicula*, 27 February 1844, and show the characteristic form correctly.

Gray and Vérany place *Octopodoteuthis* in the family Onychoteuthidae because of the biserial arrangement of the hooks on the arms. After Pfeffer had separated the family Enoploteuthidae from the Onychoteuthidae, this genus was placed in the Enoploteuthidae. However, there are a
140 number of characters which show that this is not justified.

A gelatinous consistency of the body does not occur in other Enoploteuthidae. However, this is not important because a gelatinous consistency occurs also in other families and also in juvenile forms of *Pterygioteuthis*.

More important is the absence of luminous organs because all known Enoploteuthidae have such organs. After a thorough examination for luminous organs of a young specimen from Messina, I can

state the following. Each eye bears a small, knoblike process on the ventral side which contrasts by its sheen from the surrounding tissue. Sections of this part showed, however, that this is not a deeply situated luminous organ but that lamellae which cause the iridescent or golden sheen of the eye converge toward the protruding part of the eye and cause a thickening of its outer wall.

However, I found in another region of the body, namely near the ink sac, organs which are probably luminous organs.

The oblong-oval ink sac is situated obliquely to the longitudinal axis of the body and its anterior ventral side is situated on the two large sacs of the vena cava. Its shining envelope of connective tissue is interrupted on both sides by the veins of the ink sac. A short way before the point where they open into the venous sacs, the veins of the ink sac are also covered with appendages and form small, distinct sacs. The mid-intestine passes to the left of the ink sac and then bends almost at a right angle where it passes into the hind intestine which continues anteriorly on the median surface of the ink sac. The hind intestine shows longitudinal folds and forms the two anal processes. As neither Weiss (1889) nor Appellöf (1889, p. 25) have described these structures in detail, it should be added here that each of the anal processes has an asymmetrical form and bears dorsally a wide, crescent-shaped lateral lobe.

Near the border between mid- and hind intestine, there are whitish, knoblike thickenings, 1 mm wide, embedded in shallow pits on the ink sac on both sides before the exit of the veins of the ink sac. Closer examination showed that they consist in part of lens-shaped thickenings of the hand-shaped musculi recti abdominis (musculus adductor pallii medianus). These "muscular warts" were noted by Appellöf (p. 20, Figure 13). The muscular bands are united behind them and extend to the ventral surface of the visceral sac. The thickenings bear a whitish layer on the side which faces the ink sac which is obviously not muscular, and I therefore made longitudinal sections of this formation. They showed that the lens-shaped body is formed mainly by a swelling of the smooth longitudinal musculature, which may be 0.4 mm thick (the abdominal muscles are only 0.1 mm thick). Below the swelling
141 and distinctly differentiated from it is a convex layer, 0.3 mm wide, which projects in the form of a cap toward the ink sac and consists of dense, spherical nuclei. There are no recognizable boundaries between the cells but fine capillaries which collect into a vein which extends posteriorly and apparently joins the abdominal vein. This formation is enveloped toward the ink sac by wide-meshed connective tissue.

The nature of these peculiar organs is not known. The organs correspond topographically to the large luminous organ embedded in the ink sac of *Chiroteuthis* and *Corynomma.* If these organs are luminous organs, it must be assumed that they are in a stage of beginning development and do not yet have reflectors or other accessory formations. As our specimen has genitalia like those of a larva, the condition of its luminous organs may correspond to that in *Doratopsis* (Plate XLVII, Figure 3, *luc.*).

The knoblike thickenings do not serve for compression of the ink sac, as Appellöf thought. Such a compression would only be possible if the muscle bands were arranged as constrictors. That lens-shaped thickenings of the musculature are present in front of a luminous organ is not surprising because an analogous formation of the mantle musculature is present in *Thaumatolampas* (p. 63).

The presence of a biserial arrangement of hooks on the arms of *Octopodoteuthis* has been considered as proof that this genus belongs to the Enoploteuthidae. I would accept this if *Octopodoteuthis*

had also other characters of the Enoploteuthidae. But as no other important characters of *Octopodoteuthis* agree with those of the Enoploteuthidae, the systematic importance of the hooks should not be overestimated, especially after the recent discovery of a hook-bearing genus in the Cranchiidae. Although Steenstrup and other authors considered this character as very important, this character should not be considered as decisive.

The tentacles have a peculiar form. From the well-known descriptions of Krohn and Vérany and the more detailed studies of Appellöf, we know that the tentacles disappear with age and are no longer present in large specimens. A similar phenomenon is known for *Chaunoteuthis*, *Taonius* and *Leachia*. I consider this loss of the tentacle to be less important systematically than the form of the club. As will be shown in the description of the juvenile forms, the tentacle club is short and bears only 4 pairs of suckers. As described by Appellöf, the two small proximal suckers correspond to the carpal part,
142 and the 3 other pairs of large suckers form the hand part. This differs from the condition in the Enoploteuthidae and in the Oegopsida in general: the suckers of the club form there numerous oblique rows of 4 or more suckers. The biserial arrangement in the proximal area of the hand part is sometimes caused by suppression of the marginal suckers, but this is a secondary phenomenon which takes place during postembryonic development. The condition of *Octopodoteuthis* is quite different: the club remains in a primitive state, like that in the embryos or freshly hatched larvae of other Oegopsida. In the description of the postembryonic development of the Enoploteuthidae we mentioned the condition of the club of the youngest larvae, in which the suckers are few and biserial. We may therefore assume that the club of *Octopodoteuthis* remains in this stage throughout life. At any rate, it is interesting that this small number of alternating suckers is sufficient to form a carpal part and a hand part.

Octopodoteuthis differs markedly from the Enoploteuthidae in the structure of the buccal funnel. All Enoploteuthidae have a well-developed buccal funnel with 8 points. Although the systematic value of this character has not been stressed so far, I consider it so important that I use it for the diagnosis of the family. All other Oegopsida have only 7 or 6 buccal pillars, because of the fusion of the dorsal or also of the ventral pillars. The latter condition is characteristic for *Octopodoteuthis*, as noted by Jatta and which I confirmed. The buccal membrane is delicate, with smooth inner side; it does not form points. There are 6 pori aquiferi, of which those situated between the 3rd and 4th arms are reduced to holes so narrow that we could demonstrate them only by means of a fine probe. Furthermore, it is noteworthy that the inner membrane of the tip is not fluted, as in the Enoploteuthidae, but is covered with wartlike tubercles.

The attachment of the 4th arms shows other important differences. This attachment is dorsal in the Enoploteuthidae but ventral in *Octopodoteuthis*.

According to Jatta's data (p. 94, Plate XIII, Figure 8), the radula differs from that of the Enoploteuthidae. The radula consists of 7 transverse rows in the Enoploteuthidae, with the formula 3, 2, 2, 1, 2, 2, 3, as in *Thaumatolampas*, *Abraliopsis*, *Pterygioteuthis* and *Pyroteuthis*. The radula of *Octopodoteuthis* consists of only 5 transverse rows with the formula 3, 2, 1, 2, 3. Jatta apparently overlooked the data published by Appellöf (p. 23), who gives a different formula but also noted the differences from the Enoploteuthidae.

Jatta stated that the gladius resembles that of *Loligo*, while Appellöf stated that it has a flat cone. I found that the funnel cartilage resembles the simple cartilage of the Enoploteuthidae but is wider and shows a flat pit which widens posteriorly.

Because of all these characters it seems justified to remove *Octopodoteuthis* from the Enoploteuthidae and to establish a new family for it with the following diagnosis:

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Veranydae

Body gelatinous, without luminous organs. Arms with 2 rows of hooks. Tentacles small, deciduous. Club with a small number of biserial suckers. Six buccal pillars; 4th arms attached ventrally. Radula with 5 transverse rows of teeth. Funnel cartilage wide, with a shallow pit which widens posteriorly. Gladius as in *Loligo*.

I cannot add much to the description of the inner anatomy given by Appellöf. However, I would like to mention two points which will complete the picture.

The outer openings of the renal sacs are clearly visible as a slightly curved slit on an oval papilla. The papilla projects into the renal sac in the form of a small, indented knob, also with a distinct slit. The body cavity projects toward this papilla in the form of a broad funnel which opens in a long slit into the renal sac.

The second point concerns the genitalia of *Octopodoteuthis*. All the specimens known are males. The well-preserved specimen from Messina is 58 mm long, the dorsal mantle length is 26 mm and both fins together are 33 mm wide. The testis forms only a thin ridge which is covered by the very large stomach. Only after cutting the vessels at the base of the gills did the gonoducts become visible in the form of a minute knob on the left side which is barely 1 mm wide. This proved to be the "anlage" of the gonoducts. It is apparently a very early "anlage", because the genital pocket is distinct and the duct was coiled in the initial part, whereas the ducts form undulate lines in the "anlagen" in females. At any rate, sexual maturity occurs late, because this specimen, although not small, had markedly retarded genitalia.

I mention the genitalia mainly because some authors (Jatta, Pfeffer) consider the flask-shaped swellings of the 8 arms to be symptoms of hectocotylization. I agree with Appellöf, who rejects this; Pfeffer (1908, p. 74) also recently abandoned this interpretation. The swellings are analogous to the swellings at the tips of the ventral arms in both sexes of *Abraliopsis*. If this were a case of hectocotylization, it would be difficult to understand why it should occur such a long time before sexual maturity. I have stated before that the left ventral arm of *Pterygioteuthis* shows unusually early indications of hectocotylization. However, in *Pterygioteuthis* the male genitalia are also well developed, while in
144 *Octopodoteuthis* this is not the case. It seems impossible that hectocotylization is already completed while the gonads are still at a very early stage of development. Moreover, a pear-shaped swelling is already present on the 2nd arms of one of the larvae described below. This swelling is thus apparently a character of the genus but not a phenomenon of hectocotylization.

Larval stages of *Octopodoteuthis*

(Plate XVII)

Five larvae, found by the expedition in the warmer currents of the Indian Ocean, undoubtedly belong to the genus *Octopodoteuthis*.

These larvae were caught in the following localities:

Station 102: Agulhas Current, 34°31′ S, 26°00′ E. Vertical net to 1,800 m. Two medium-sized larvae.
Station 190: Inner Sea of West Sumatra, 0°58′ S, 99°43′ E. Vertical net to 1,100 m. One small larva.
Station 215: Indian North Equatorial Current, 7°1′ N, 85°56′ E. Vertical net to 2,500 m. One small larva.
Station 271: Gulf of Aden, 13°2′ N, 46°41′ E. Vertical net to 1,200 m. One large larva.

The oldest larva (Figures 1 and 2) was caught in the Gulf of Aden. Its characteristic form resembles that of the adult so closely that the characteristics of *Octopodoteuthis* are clearly discernible. It is 8.5 mm long and the dorsal mantle length is 4.7 mm. Its body is plump, gelatinous, with relatively large, transparent fins which are connected dorsally and are together 8 mm wide. The dorsal base of the fins extends to about half the length of the mantle, which is less gelatinous than in the adult. The mantle corners project only slightly ventrally and are blunt dorsally. The characteristic form of the head is due to the large eyes, which have wide, thick stalks. The large optic ganglia are situated in the base of the stalks. The eyes diverge markedly, the head is 3 mm wide and each eye is 1.1 mm wide.

The **arm apparatus** is situated on a conical pillar. It differs from that of the adult in the strong development of the tentacles, which are 2 mm long and only slightly shorter than the dorsal arms (Figure 10).

The short, strong **stalks of the tentacles** have a flat inner side and are delimited by weak ridges from the rounded outer surface.

145 The **club** is already definitely developed and does not differ from the club of the adult illustrated by Appellöf and Jatta. It is narrow, spoon-shaped, and forms an angle of almost 45° with the stalk (Figures 7, 8). There are two wide, well-developed protective membranes with chromatophores arranged in rows. The club bears 8 alternating suckers, of which the two proximal or carpal suckers are situated on the terminal part of the stalk and are much smaller than those on the hand part. The two proximal suckers of the hand part are the largest and the others become gradually smaller. The chitinous ring of the suckers has no teeth; microscopical examination shows minute points on the ring.

The **arm** formula is 2, 1, 3, 4. All arms bear only suckers, but some suckers are lost. Of particular interest is the knoblike swelling only at the tips of the 2nd arms. This is apparently the terminal swelling which is characteristic for the arms of this genus. This is certainly not hectocotylization, because of the small size of the larva and the embryonic condition of the gonads.

The **buccal cone** is chimney-shaped and has a fluted inner lip. The buccal membrane is situated flat on the bases of the arms and is distinctly hexagonal (Figure 10).

The **funnel** is relatively small and does not reach beyond the optic ganglia.

This larva is transparent so that its inner organization is visible. The large statocysts are visible between the two optic ganglia at the level of the base of the funnel. The liver, the ink sac near the hind intestine and the anal appendages are also visible. The stomach is situated behind the gills and almost reaches the posterior end. It has a well-developed caecum.

We have two slightly younger larvae from Station 102 in the Agulhas Current of the Indian Ocean. They differ in several aspects from the larva described above. The larger larva (Figures 3 and 4) is 7 mm long (including the tentacles) and the dorsal mantle length is 3.8 mm. It is slightly plumper than the larva described before; the posterior end is more rounded and the mantle is relatively wider. The rounded fins are much smaller and are not connected dorsally; they are little longer than a third of the mantle length. The eyes have thick stalks; they are 0.6 mm wide and are relatively smaller than those of the older larva.

The tentacles (Figure 9) are 2 mm long and are longer than the 2nd arms, but otherwise they do not differ from those of the previously described stage: they also bear 8 suckers, of which the two carpal suckers are much smaller than the others.

146 The arm formula is 2, 1, 3, 4; however, the 4th arms are relatively shorter than in the older stage. The 1st, 2nd and 3rd arms bear suckers which form conical points. I thought at first that this was a

transformation into hooks, but microscopical examination showed that these are very long suckers with a narrow opening and their chitinous ring does not form a hook. These suckers are apparently just about to be transformed into hooks.

Only the anterior part of the body of the younger specimen from the same station is shown in Figure 5 and 6 (ventral and dorsal view). This larva is 5.3 mm long (including the tentacles) and the dorsal mantle length is 2 mm. The eyes have thick stalks in the bases of which are situated the large optic ganglia. Behind them are the relatively large statocysts, which are contiguous in the middle and contain shining statoliths. The head is conical, and the tentacles are markedly longer than the other arms. The club is clearly delimited from the stalk and markedly narrower. It bears 4 suckers which decrease in size toward the tip and 2 small carpal suckers. The tips of some arms are missing, but the 2nd arms are the longest and the 4th arms the shortest; the formula here, too, is apparently 2, 1, 3, 4. The few suckers on the arms show no indication of a transformation into hooks. The buccal cone is chimney-shaped, with a distinctly fluted inner lip.

If the two larvae from the Agulhas Current are compared with the older larva from the Gulf of Aden, it appears that the body is plumper, the fins smaller, the stalks of the eys longer and the eyes relatively smaller. The tentacles are longer than the other arms.

I have two other larvae, which are much smaller and apparently freshly hatched. They were collected in the Indian North Equatorial Current and in the inner sea of West Sumatra. The length of the larvae is 2.8 and 2.2 mm, the mantle length 1.7 and 1.2 mm. Despite their minute size, these specimens clearly show the characteristics of *Octopodoteuthis*, as is seen in Figure 11 which shows the anterior part of the youngest larva. The stalks of the eyes are still more prominent than in the older stages, while the arm apparatus is in a very primitive condition. At any rate, the larva certainly belongs to *Octopodoteuthis*, as shown by the form of the tentacles, which are short and strong but longer than the other arms; the 3rd and 4th arms form short cones, while the 1st and 2nd arms are slightly longer but bear only a single sucker.

The tentacle club bears 5 suckers (Figure 12). The two small proximal suckers belong to the carpal part; then follow two very large and a smaller distal sucker which form the hand part, which already forms an angle with the stalk. Although the fins are lost, they are certainly very small, to judge from their dorsal attachment.

147 As all larvae were collected in the Indian Ocean, they are probably developmental stages of the same species. On the other hand, the oldest stage (Figures 1, 2) differs from the slightly younger stage (Figures 3, 4) not only in the relative size of the fins and arms but also in the very large eyes. Another distinctive character of the younger larva is the apparently early transformation of the suckers on the arms into hooks. These differences may indicate that some of the larvae belong to *Octopodoteuthis sicula* and the others to an unknown species. This, however, cannot be decided on the basis of the available material.

3. Family **Histioteuthidae** Verrill, 1881

(Plates XVIII, XIX, XX, XXI)

Loligopsidae d'Orbigny, *Céph. cét.*, 1835–48, p. 320 p. p.
Loligopsidae d'Orbigny, 1845, 1855, p. 367 p. p.
Chiroteuthidae Gray, 1849, p. 42 p. p.
Loligopsidae Vérany, 1851, p. XI p. p.
Taonoteuthi Steenstrup, 1861, p. 1.
Histioteuthidae Verrill, 1881, p. 431.
Taonoteuthi subf. *Chiroteuthidae* Hoyle, 1886, p. 42 p. p.
Taonoteuthi Goodrich, 1896, pp. 12, 15 p. p.
Taonoteuthi Jatta, 1896, p. 114 p. p.
Taonoteuthidae subf. *Histioteuthinae* Joubin, 1900, p. 88.
Histioteuthidae Pfeffer, 1900, pp. 152, 168.
Histioteuthidae Hoyle, 1904, p. 42.
Taonoteuthi subf. *Histioteuthidae* Fischer and Joubin, 1906, p. 341.
Histioteuthidae Pfeffer, 1908, p. 75.
Histioteuthidae Hoyle, 1909, p. 271.

HISTORICAL NOTES

Among the new Cephalopoda discovered by Vérany in the Mediterranean, the genera *Histioteuthis* and *Chiroteuthis* are of particular interest. The connection of the arms by a large membrane, the large head with its enormous eyes, the magnificent purple coloration, the phosphorescent light of the luminous organs, described enthusiastically by Vérany, make *Histioteuthis* one of the most beautiful forms of the Mediterranean deepwater fauna. We know this genus from Nice and Messina. Many specimens of *Histioteuthis* and *Chiroteuthis* were caught in deep waters in the Nice area and near Messina, where peculiar conditions bring deepwater forms to the surface.

Vérany obtained the first specimen on 7 September 1834. He sent it together with a *Chiroteuthis*
148 to Férussac, who was preparing his monograph for publication. Férussac presented these two extraordinary Cephalopoda before the Académie des Sciences on 27 October 1834. He described one of them as *Loligopsis veranyi* and called the other, as suggested by Vérany, *Cranchia bonnellii*, in honor of the distinguished professor in Turin. *Chiroteuthis* is shown in Plate 65 under the old name *Loligopsis veranyi*, and Plate 65 [*sic*] shows the first illustration of a species of Histioteuthidae under the name *Cranchia bonnellii*. d'Orbigny (*Céph. acét.*, p. 327) established the genus *Histioteuthis* for this species. It is illustrated after Vérany in color (*Cranchia*, Plate 2) as *Cranchia bonnelliana* Férussac. Vérany gave a detailed description of this species (1851, pp. 114–117, Plate 19). He also describes a second species, *H. rüppellii* (p. 117, Plates 20–21), which is stated to differ from *H. bonnellii* in characteristic form and coloration. It is impossible to decide whether these are two different species of *Histioteuthis*. All specimens caught since show the violet or purple coloration of *H. rüppellii*;

deep red forms with the characters of *H. bonnellii* have not been found again. The two species are identical according to Pfeffer (1900, p. 170).

This species occurs also in the open ocean, as recorded by Verrill (1879, p. 251), who described fragments of *Histioteuthis collinsii* from the stomach of *Alepidosaurus ferox* from the east coast of the United States. His detailed description (1881, p. 234, Plate 22; Plate 27, Figures 3–5; Plate 37, Figur 5; Plate 55, Figure 6) proves that this species is identical with that found in the Mediterranean. Pfeffer (1900, p. 170) also considers *H. collinsii* as identical with *H. bonnelliana.*

Many specimens of *Histioteuthis* have been found since in the Atlantic Ocean, particularly near the Azores, from where Joubin (1900, p. 98) described 3 well-preserved specimens from the stomach of a sperm whale, which shows that the whale had to dive deep to a catch the large *Histioteuthis*, probably betrayed by its phosporescence. The thermocline, in which the temperature falls rapidly by 5–7°, is at a depth of 170–200 m in these areas. We must therefore assume that whales hunt in such depths, where the pressure is 18 atmospheres. At any rate, viable specimens of *Histioteuthis* have not been found at the surface, except in the port of Messina; animals found at the surface are always dead and usually damaged by oceanic birds, as reported by Fischer and Joubin (1906, p. 341) also from the Azores.

There are different views on the systematic position of *Histioteuthis.* d'Orbigny places the genus
149 in the Loligopsidae, Steenstrup in his group Taonoteuthi, which he established in 1861. Steenstrup never gave a definition of the Taonoteuthi, and we therefore refer to later authors, especially Hoyle (*Challenger Report*, 1886, p. 42) who placed *Histioteuthis* in the Taonoteuthi. Jatta (1896, p. 40) and Joubin (1900, p. 88) retained the Taonoteuthi without, however, attempting a diagnosis.

Verrill (1881, p. 431) established the new family Histioteuthidae for the genus *Histioteuthis.*

Other pelagic deepwater forms have been found since which show definite relationships to *Histioteuthis.* From the catch of the "*Challenger*", Hoyle (1885, *Diagnoses*, II, p. 201, *Prelim. Rep.*, 2, p. 306; 1886, *Chall. Rep.*, p. 180, Plate 30, Figures 9–15) described the genus *Histiopsis*, from the southern Atlantic. However, I agree with Pfeffer, who considers *Histiopsis* as a juvenile form of *Histioteuthis*; I shall explain this later in detail.

The genus *Calliteuthis*, established by Verrill in 1880, differs distinctly from *Histioteuthis* in several characters.

Calliteuthis reversa Verrill (1880, *Amer. Journ. Sc.*, XX, p. 393; 1880, *Proc. Nat. Mus.*, III, p. 362; 1881, p. 295, Plate 46, Figures 1–1b) apparently occurs in all oceans: specimens are known from the Mediterranean, the east coast of the United States, the Andaman Islands and the Pacific Ocean. *Calliteuthis ocellata* is a large species described by Owen (1881, pp. 139–143, Plate 26, Figures 3–8; Plate 27) as *Loligopsis ocellata* from the Sea of Japan. I have examined another Japanese specimen caught by Doflein in Sagami Bay and can add a number of details to the description. The specimen, a mature male, is the largest specimen of *C. ocellata* obtained so far.

Other species of *Calliteuthis* were described by Goodrich (1896, p. 15, Plate 4, Figures 62–71) as *Histiopsis hoylei*, and by Pfeffer (1900, p. 170), who named a form from the west coast of Central America *Meleagroteuthis hoylei.* Pfeffer divided the genus *Calliteuthis* into the genera *Meleagroteuthis*, *Stigmatoteuthis* and *Calliteuthis*, mainly according to the distribution of the luminous organs. This may justify the establishment of new species but not of new genera.

Verrill (1881, p. 430) placed the new genus *Calliteuthis* in the Chiroteuthidae, while Hoyle placed it in the group Taonoteuthi. Pfeffer recognized the close affinities of this genus to *Histioteuthis* and placed it in the family Histioteuthidae—correctly, as we shall show in the description of this genus.

Little is known about the inner structure of the Histioteuthidae. Weiss (1889, Plate 10, Figures 8–

12) described the mantle complex of a female *Histioteuthis* from Messina; JOUBIN gave the first
150 detailed description of the luminous organs of a species of Cephalopoda, i.e. of *Histioteuthis* and *Histiopsis* (1893, 1894–1895).

Nothing is known so far on the genital conditions of the family and particularly on the hectocotylization of the males of Histioteuthidae. The following description will shed some light on these aspects. The structure of the "sail" (web) and other external characters of this remarkable group will also be described.

External characters

1. Mantle and Funnel

The body is gelatinous, vividly pigmented and bears numerous luminous organs. The **mantle** is goblet-shaped, short and wide in *Histioteuthis*, slightly narrower in *Calliteuthis*. It has a gelatinous cutis. The musculature is tough and well developed in *Histioteuthis*; it is softer in *Calliteuthis* because of much gelatinous tissue between the radial septa. The 3 mantle corners project only slightly and the indentation between the ventral corners is weakly developed. The posterior end of the body is pointed conical. The fins are set obliquely because their base is situated more laterally anteriorly, while they extend in a curve posteriorly on the dorsal surface, but without reaching the posterior end of the body. The fins are connected posteriorly in a wide, heart-shaped indentation, so that the apex of the body is free and sometimes may project slightly beyond the fins. PFEFFER (p. 168) attributes this condition to an injury, i.e. separation of the fins from the posterior end of the mantle. In fact, this condition is quite normal, as shown by medium-sized specimens. On the other hand, the whole posterior end of the body is fused dorsally with the fins in old specimens, i.e. in the two large males of *Histioteuthis* and *Calliteuthis*. It is difficult to decide at present whether this different condition is due to specific differences or whether it varies with age or sex. Thus, a medium-sized, almost mature female has a free posterior end which projects slightly beyond the fins; as stated above, such a condition does not occur in old males.

The **fins** are relatively small in young animals; they reach half the length of the mantle in old specimens.

The **funnel** is relatively small and slightly narrower toward the opening. The adductors are fused on each side into a muscular lamella which projects distinctly. There is a small valve, but a deep funnel groove is absent.

The **funnel organ** has distinct margins. It consists of 2 long oval ventral parts and an angular, bowed dorsal part; the dorsal part is twice as long as the paired lateral parts in *Calliteuthis*.

The various locking cartilages may be described as follows. The **mantle cartilage** of *Histioteuthis*
151 is sword-shaped, slightly curved, with a wide posterior end and pointed anterior end; its convex side faces the dorsal surface. This cartilage is 32 mm long in the large male. In *Calliteuthis*, it resembles that of *Histioteuthis* but is less curved.

The **funnel cartilage** forms a deep groove which is narrower anteriorly and forms a negative of the mantle cartilage; the groove is thus also sword-shaped in *Histioteuthis*. The margin of the cartilage is folded over in old specimens; it is 32 mm long and 12.5 mm wide.

The **neck cartilage** (Plate XX, Figures 2, 4) is always spatulate, wider anteriorly. It bears in the middle a cartilaginous ridge, with a groove its whole length. In some species of *Calliteuthis* this groove is slightly shallower and the spatulate widening of the anterior end is only weakly indicated. The cor-

responding cartilage on the mantle has a narrow anterior end and a median ridge which fits into the groove of the neck cartilage. The neck cartilage is 21 mm long in the large specimen of *Calliteuthis ocellata* and 31 mm long in *Histioteuthis*.

2. Head and Neck

The **head** is wider than the mantle already in young specimens; it becomes very large in older specimens, because of the very large eyes.

A sharp, projecting edge separates the head from the **neck** laterally and ventrally (Plate XXI). This edge forms a curve that is convex anteriorly around the funnel, which is therefore situated in a pit but projects like a wall toward the posterior margin of the eyes. It meets dorsally a shorter wall which together with the former forms a flat, almost triangular cervical pit in which the olfactory tubercle is situated in the middle. These conditions apply especially to the large male of *Histioteuthis*, but also to the old male of *Calliteuthis*, although here the margins of the wall are not so sharply differentiated.

The olfactory tubercle of *Histioteuthis* is situated in the middle of the lateral cervical pit, on a transverse fold which is 7 mm long and extends slightly posteriorly in the area of the tubercle. This area is covered at the margin with olfactory epithelium which is 4 mm long and forms a distinct, whitish, sickle-shaped layer.

The olfactory tubercle of *Calliteuthis* is also situated on a fold which, however, projects more steeply and bears only 2 mm of olfactory epithelium. The olfactory tubercle is situated here close to the ventral swollen ridge.

These are certainly transverse folds which run obliquely, except the fold which bears the olfactory tubercle in *Histioteuthis*. The smaller dorsal wall corresponds to the first transverse fold, the large fold situated ventral to the funnel corresponds to the 3rd transverse fold, and the fold with the olfactory tubercle to the 2nd transverse fold.

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3. The Eye

The **eyes** are very large; the lens of the male of *Histioteuthis* is 26 mm wide, while the slightly collapsed eyeball is 45 mm wide. The lid margins are circular, with a weakly developed anterior sinus which is more distinct in the large specimen of *Calliteuthis ocellata*.

The **eyeball** of *Histioteuthis* is spherical, that of *Calliteuthis* conical in the single specimen examined, a young *C. hoylei*. This may be the beginning of a transformation into a telescopic eye which is perhaps even more marked in the adult animal. The eye (Plate XX, Figure 1) is 8 mm long and 6 mm wide, i.e., the ratio of the longitudinal axis of the eye to the width in cross-section is 4:3. The ciliary region and iris are steeply raised because of the conical or ovoid form of the eyeball. Clearing in oil of cloves shows the purple envelope of pigment inside the eye which extends to the equator of the lens below the epithelial body. The retina forms a flat, dishlike area only on the posterior side of the eyeball and leaves the lateral walls free. The large optic ganglion (*g. opt.*), which is situated on the inner side of the eyeball, is 3.5 mm wide and 1 mm thick; it is surrounded laterally by the bandlike, slightly crinkled white body (*c. alb.*).

I made sections of the eye of *C. hoylei* which show the following details. The eyeball consists of

a delicate envelope of connective tissue in which a wide but thin cartilaginous ring is embedded at the margin of the retina. There are no other cartilaginous formations in the eyeball or in the iris. The posterior side of the eye has a very thin sclera, which forms a hyaline lamella.

The **iris** is covered by undulate lamellae of connective tissue as a direct continuation of the delicate sclera. These lamellae cause the metallic sheen due to structural colors. The middle layer of the iris is formed by a thin circular layer of muscles which becomes thicker toward the free outer margin and forms a sphincter the fibers of which extend outward to the undulate strands of connective tissue. The inner surface, which faces the lens, consists of a fine granulate pigment in polyhedral cells with large spherical nuclei.

The **muscles of the eye** are weakly developed. They form a muscular ring which surrounds the eyeball on the outside as a continuation of the circular musculature of the iris and is thickened into a strong sphincter on the outer side at the base of the epithelial body.

The very delicate ciliary muscle, or Langer's muscle, is attached to the basal margin of the wide epithelial body and consists of longitudinal fibers which extend to the inner margin of the ring of cartilage. This ciliary muscle is covered by the circular musculature of the eyeball on the outside.

153 The **lens** of the preserved specimen is thicker in its longitudinal axis than in its transverse axis; it is difficult to decide whether this is natural. The lens is relatively large, 3.3 mm wide, and the epithelial (ciliary) body which secretes the lens is therefore also thick.

The **vessels of the eye** consist of an arterial and a venous ring, as shown by sections; both vessels are situated at the base of the epithelial body, the arterial ring distal to the venous ring. Also visible are large veins between the white body and the optic ganglion.

Of special interest is the **retina.** It forms a flat dish—which is thinner at its margin—at the posterior side of the eyeball, without covering the eyeball's lateral walls. The inner sides of these walls are covered with a dark pigment, being a continuation of the pigment of the retina. The fibers from the optic ganglion pass through a fine-meshed connective tissue and extend to the sensory epithelium as separate fascicles. The layer of sensory cells is 0.1 mm thick in the center of the retina. Although the sensory epithelium forms a single layer, the elements are so thin and densely arranged that their very small spherical nuclei are situated at different levels and there may be up to 15 nuclei above each other, mainly in the center of the retina. The sensory epithelium of *Calliteuthis* has a finer structure than that of *Benthoteuthis*. The nuclei of the cells of the membrana limitans are 3 or 4 times as large as those of the visual cells; there are 2 or 3 nuclei layered above each other in the center of the retina. Then follows inward a relatively thin layer of pigment which continues laterally on the lining of the eyeball. The rods contain no pigment; they are very thin and 0.17–0.18 mm long in the center of the retina; they become gradually shorter and wider toward the margin.

The eye of *Calliteuthis* thus shows a typical adaptation to life in deep water: the retina covers only the posterior side of the eye and consists of finer and more densely arranged elements than found in the so-called stripe which characterizes the forms living at the surface. Moreover, the pigment occupies the position associated with total darkness: it is restricted to a narrow stripe along the cells of the membrana limitans.

4. Arm Apparatus

The **arm apparatus** is moderately developed in young specimens but very strongly developed in old specimens. The 8 arms are of about the same length. The 3rd or 4th arms, sometimes also the

1st arms, may be the longest, but the differences are not marked. The arms bear sharp edges which are more strongly developed on the dorsal arms.

Swimming membranes are weakly developed. The swimming membrane forms a horny keel on the 3rd arms of an old *Histioteuthis*. The swimming membranes of *Calliteuthis* extend along the
154 whole arms and pass at the base into those of the adjacent arms, but they do not become wider. There are also membranes on the outer side at the base of all arms. These membranes are indistinct in young and distinct in older specimens. These membranes have not been described in the Oegopsida and I name them **outer membranes**, because they are not related to the protective or swimming membranes. As the protective membranes of *Calliteuthis* are fused at the base, there are pockets between the outer membranes and the bases of the arms. The extended arm apparatus of a large *Calliteuthis* has thus a large membrane at the base which is formed entirely by these outer membranes.

Histioteuthis is characterized by such a large membrane ("**sail**"). Férussac and Vérany showed that this "sail" is a strong, muscular cutaneous membrane which surrounds the 1st, 2nd and 3rd arms, so that the tentacles and ventral arms are situated outside. However, the ventral arms are also connected with the "sail" by their ventral protective membranes, which extend toward the base to the ventral median side of the "sail" on each side, where they are either connected by a sharp ridge, or they diverge and are fused separately with the ventral side of the "sail".

Nothing has been published on the morphological interpretation of this "sail". Is this a structure sui generis? Or has it developed from membranes present also in other Oegopsida? I answered this as follows in an earlier publication (1906, p. 744). The ventral protective membranes of the ventral arms are unusually developed toward the "sail" and finally become fused with its ventral surface. Such protective membranes are apparently absent on the 1st, 2nd and 3rd arms but in fact they are present, near the apex of the arms, and then become gradually wider and pass into the "sail".

It follows that the "**sail**" must be morphologically interpreted as consisting of **very large protective membranes.** The ventral arms, which are situated outside the "sail", have normal protective membranes in the distal half; the ventral protective membranes of these arms are widened on one side and extend to the ventral surface of the "sail".

As in *Calliteuthis*, the wide outer membranes between the bases of the arms of *Histioteuthis* form 8 pockets between the "sail"-like protective membranes, the outer membranes and the bases of the arms. The outer membranes between the 3rd and 4th arms border also on the base of the tentacles which are situated in their pockets.

The **tentacles** show a rather uniform structure in the whole family. They are short, strong, three-edged, with a widened club the tip of which is curved dorsally like a chamois horn. The swimming membrane is reduced to a distal keel which is displaced dorsally. The protective membranes are very weakly developed.

155 The suckers of the club form more than 4, usually 6–7 longitudinal rows in the proximal part of the hand. The suckers gradually become arranged in quadriserial rows toward the tip of the club. The club of the large male of *Histioteuthis* has a very narrow distal part which bears biserial alternating rows of suckers on the ventral ridge; the suckers at the tip are arranged in 3–4 rows of 3 suckers. In the proximal part of the hand, several suckers of the dorsal median rows (about 5 pairs) are always larger than the others.

The adhesive apparatus is uniformly developed in all species. It covers the carpal part and the distal half of the stalk. Pfeffer stated correctly that the carpal part consists of a dorsal marginal row of alternating suckers and knobs which continue on the ventral side of the stalk as a ventral marginal row of alternating pairs of suckers and knobs. The suckers and knobs of the left tentacle alternate

exactly with those of the right tentacle so that a knob of one tentacle fits into a corresponding sucker of the other tentacle.

The **suckers on the arms** are biserial; those in the middle of the arm are large and almost spherical. In a large male of *Calliteuthis ocellata*, the suckers are 7 mm wide, in *Histioteuthis* even 8 mm wide. The smallest suckers are situated on the ventral arms; the largest suckers are 5 mm wide in *Histioteuthis* and only 2 mm wide in *Calliteuthis*.

The suckers of *Histioteuthis* usually have short stalks and have no large teeth at the margin. Those of the club are finely toothed all around, while the suckers on the arms have only 2–4 crescent-shaped broad indentations. The suckers on the arms of *Calliteuthis* may have teeth or not, or they are replaced by indentations.

Examination of a sucker from the opening shows that this is surrounded by a thick circular pad which is slightly wider dorsally and sometimes even covers the chitinous ring. Under the magnifying lens, the ring has a honeycomb pattern or a system of meandering lines.

Median longitudinal sections of a sucker of *Calliteuthis ocellata* show that the short stalk is situated on a wide gelatinous cone with a central nerve which forms a small ganglion at the entrance into the sucker. The sucker consists of gelatinous tissue which forms not only the sucker itself but also the large pad. The gelatinous tissue contains radial fascicles of fibers which are connected by branches with the adjacent fascicles. In addition to these radial fibers, the circular systems of fibers appear in cross section at the posterior wall of the sucker. Such systems are also present around the opening in front of the chitinous ring. This stains intensively with various stains and shows under oblique light a radial striation which is apparently caused by prisms given off by underlying cells. The epithelium which forms the chitinous ring is cylindrical only at the margin of the ring but flattened otherwise. On the pad near the opening of the sucker, it passes into a high, glandular, cylindrical
156 epithelium. The cells have oval nuclei in the middle near the cell wall; they are almost entirely filled with a secretion which consists of light-colored granules or of homogeneous masses.

FIGURE 22. Median longitudinal section of the distal part of a sucker on the arm of *Calliteuthis ocellata* OWEN (microphotograph)

The sword-shaped chitinous ring is situated on the pad, which is covered with glandular epithelium. The upper outer surface of the sucker bears the pits with glandular epithelium.

The most remarkable modification of the epithelium is present near the outer surface of the sucker in the area of the ring-shaped pad. There are numerous pit-shaped depressions on the broad dorsal surface of the pad which are lined with a high glandular epithelium the cells of which are filled with

fine, refractile granules, like those of the pad. Between these cells are bottle- or club-shaped cells, resembling the diffuse mucus cells of molluscs. The oval or spherical nuclei of these cells lie mainly at the base; there are also peripheral nuclei at many points which may be supporting cells. The boundaries of all the bottle-shaped cells are indistinct. However, this is certainly a cylindrical glandular epithelium which lines a dense honeycomb pattern of small glandular pits that very likely secrete a poison.

5. Buccal Funnel and Its Attachment

The attachment of the arms of the Histioteuthidae shows a number of special characters. The buccal funnel is supported by 7 buccal pillars in *Calliteuthis*, especially in the mature male of *C. ocellata*, and in young specimens of *Histioteuthis* (Plate XX, Figure 3). Each buccal pillar is widened in the middle and is so transparent that the thick nerve inside it is visible. The pillars end in 7 projecting points at the margin. Pfeffer stated that old specimens of *Histioteuthis* have only 6 such points. This reduced number of buccal points is caused by the fusion of the ventral buccal pillars, so that its origin from 2 pillars is not recognizable.

The **buccal membrane** forms a roof above the base of the arms and is fused with the pharynx. From the buccal pillars extend attachments to the arms; they form 6 shallow spaces between the base
157 of the arms and the lower surface of the buccal funnel. These cavities or **buccal pockets** are completely separated and open to the outside through slit-shaped openings, usually named pori aquiferi. In the old *Histioteuthis*, the outer margins of the lateral buccal pockets are fused with the basal part of the "sail", so that there are only 4 pori aquiferi. The buccal funnel is smooth on the outside; in adult specimens its inner surface bears longitudinal grooves. The attachments for the arms extend from the buccal pillars. The dorsal buccal pillar has a divided membrane of attachment which extends to the dorsal side of the 1st arms. The other attachments are dorsal on the 2nd arms, ventral on the 3rd arms, and again dorsal on the 4th arms. All attachments pass laterally along the base of the arms without direct connection with the protective membranes. In the old specimen of *Histioteuthis*, which has only 6 buccal pillars, the ventral attachment, like the dorsal attachment, is divided to both respective arms. The attachment of the arms is thus the same as in the Enoploteuthidae and in the other families (p. 15). The tentacles also have a muscular attachment, which is particularly long, on the inner side.

The **buccal cone** is well developed (35 mm wide in the large male of *Histioteuthis*) and the jaws are large. The outer lip of the adult *Histioteuthis* is very wide, like the inner lip; both lips bear longitudinal grooves.

6. Gladius

The **gladius** of large specimens has not been described. The following description is based on the gladius of the adult male of *Calliteuthis ocellata* (Figure 23).

The rhachis tapers slightly toward the dorsal mantle corner. It is widest behind the corner and then gradually tapers posteriorly. The rhachis has no sharp ridges and is slightly convex. The vane begins a short distance behind the anterior part of the rhachis and then widens so that the gladius, which is 140 mm long, is 38 mm wide in the middle. The vane narrows posteriorly and ends in an oval curve without indication of a cone.

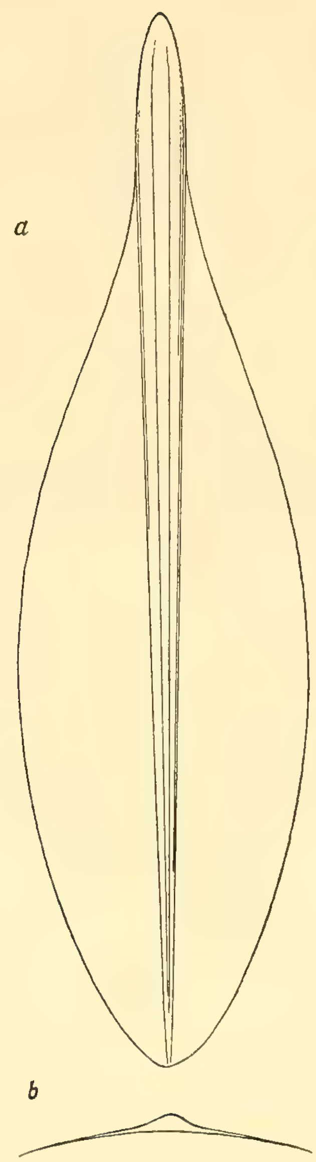


FIGURE 23. Gladius of *Calliteuthis ocellata* OWEN (natural size): *a* dorsal; *b* cross section.

158 7. Coloration

All Histioteuthidae have a brilliant **coloration.** The key hue, which is red or dark violet, is caused not only by the numerous chromatophores but also by the granulate pigment in the cutis. Pale violet specimens, like the large specimen of *Calliteuthis ocellata*, too, get their splendor from the numerous luminous organs which appear like jewels on the skin. According to VÉRANY, the organs of the live *Histioteuthis* gleam like pearls, with a blue margin and with a mirror with a mirror with a golden sheen anteriorly. This vivid coloration extends over the whole body except the fins, which are always paler. The tentacles, too, are generally less lightly colored than the arms. The inner surface of the arms is lighter, except for the sucker-bearing area surrounded by the protective membranes. The "sail" of *Histioteuthis* is intensively colored on the outside and inside. The outer side of the buccal membrane is also usually dark-violet.

It is very characteristic for the family that the coloration extends also to the inner side of the mantle and even to some inner organs. Thus, the inner surface of the mantle, the gills and parts of the abdominal wall of *Histioteuthis* and *Calliteuthis* are dark-purple or chocolate-brown, but the margin of the mantle is paler. The intestine is deep purple, and so is the esophagus, stomach and caecum of the large *Histioteuthis*. In *Calliteuthis* the purple tone is restricted to the stomach while the caecum is paler. The mid- and hind intestine are of similar color.

8. Luminous Organs

a) Arrangement of the organs

The **luminous organs** of the Histioteuthidae are especially prominent because they are all situated in the outer skin and not on the ventral side of the eyeball or in the mantle cavity.

The ventral organs are usually more numerous than those on the dorsal side. The organs on the ventral arms are much more numerous than those on the dorsal arms.

The arrangement of luminous organs provides good systematic characters. The number of rows of organs on the outer side of the arms is apparently more or less constant for the different species of *Calliteuthis*. The organs may form 3 rows on the ventral arms and a single row on the other arms, or the ventral arms bear 7 or 8 rows and the other pairs 4 or 3 rows of densely arranged organs. The organs are usually of more or less uniform size, but there may be marked differences. In the large *Calliteuthis*
159 *ocellata*, for example, the ventral indentations of the mantle margin bears 9 medium-sized organs, followed by similar organs on the lateral margin of the mantle; the next 2 transverse rows consist of larger organs, and the following organs gradually decrease in size toward the posterior end.

There is another characteristic condition which has been overlooked in the past. The lid margin bears luminous organs in a constantly asymmetrical arrangement. The organs around the right eye are always much more numerous than those around the left eye. In the large specimen of *Calliteuthis* there are 17 organs at the right eye and only 2 at the left eye. The condition is similar in other species of *Calliteuthis*, in which the left eye may even have no luminous organs, while the right eye has about 18 organs.

The right eye of *Histioteuthis* also has more luminous organs than the left. Some early observers published drawings of the right side showing a circle of numerous luminous organs, but not noticing the asymmetry. The cause of this asymmetry is not known, as the biology of these forms has been little studied.

b) Fine structure of the luminous organs (Plate XX, Figures 12–14)

The luminous organs of *Histioteuthis* were described correctly by JOUBIN in 1893 and 1894. I shall only add a number of details on the organs of *Calliteuthis*, which closely resemble those of *Histioteuthis* in all important characters. The marked polymorphism of the luminous organs of the Enoploteuthidae is absent in the Histioteuthidae. The organs of the Histioteuthidae are of uniform structure and differ only in size and in the thickness of the various layers.

I begin with the description of the luminous organs of *Calliteuthis hoylei* for two reasons: a. the conditions are simpler; b. the luminous organs of specimens of *C. hoylei* which were caught alive at the surface and were preserved in formol are in good condition.

The organs of the small *Calliteuthis hoylei* are 7 mm wide and are embedded in the cutis more

or less parallel, rarely obliquely, to the surface. They form dark, slightly projecting knobs, before which are situated 2–3, rarely more, dark chromatophores.

Median longitudinal sections (Figure 12) show the centrally situated **luminous body** (*phot.*) in the form of a cup which opens toward the outside and consists of a single layer of cells in a radial arrangement toward the main axis of the cup. The nuclei of these cells are large and spherical, with
160 uniformly distributed chromatin, and they are situated in their proximal part, i.e. near the reflector. The proximal half of the cell is situated either broadly on the reflector or projects like a spindle in the more inward situated cells; it stains intensively and has a homogeneous content which is divided into fibers toward the light-colored distal half of the cell (Figure 14). The boundaries of the cells are distinct in the proximal half and are also indicated by the regular arrangement of the nuclei. They become indistinct distally because of the fibrous structure. The central cells are usually the longest, the marginal cells the shortest. Because of the characteristic structure of the luminous cells which form the cup, the periphery of the cup is intensively stained and the inner surface is pale in preparations.

This arrangement of the luminous cells is the simplest and most primitive in the whole Histioteuthidae and therefore provides the key to an understanding of the complicated conditions in the other forms. On the opening of the luminous cup a projecting spherical **lens** (*l.*) is situated which also fills the interior of the cup with a cellular plug (*l.'*). The cells forming the lens have a characteristic structure which is difficult to understand. The central plug consists of long, almost parallel cells, but also of obliquely arranged cells in some places. These cells have long oval nuclei. They stain more intensively than the cells of the lens itself, which form a network of cells arranged in strands. The cells at the anterior margin of the luminous body are flask-shaped, while the others are short and thick, connected at the truncate and into a framework of rods with light-colored intervals. These cells stain weakly and have spherical nuclei. They sometimes show a fine striation which is caused by a concentric stratification of the cell content, as cross sections show. Cross sections of the lens cells differ markedly; they are sometimes rounded, sometimes angular. The larger cells are situated in the center of the lens, the smaller cells at the periphery, and the nuclei are therefore more numerous at the periphery of the lens.

A well-developed **reflector** (*refl.*), which consists of squamous cells (*c.sq.*), is situated next to the luminous body, toward the outer surface, as in the luminous organs of other Cephalopoda. These cells are superimposed like roof tiles in regular curves. They contain a central spherical nucleus and a homogeneous, sometimes lamellar, stratified content which stains intensively. Examination from the surface (Figure 12) shows that the spherical nucleus is surrounded by a reticulate plasma which does not reach the margin of the cell and which is indistinctly defined and often indented by the passage of capillaries (*cap.*) or nerves (*n.*). However, they often enter the interior of the cells, especially the nerves.

The squamous cells become flattened and form fibers near the luminous body. The nuclei appear elongate in sections because of the strong flattening of the cells. The cells pass gradually into fibrous
161 systems of lamellae at the inner margin of the reflector. Longitudinal sections through a row of luminous organs show that the fibrous strand (*spec.*) from the inner margin of the reflector extends to the organ situated in front of it where its tapering end reaches the outer margin of the reflector (*spec.'*). Cross sections of this area show a system of undulate lamellae of connective tissue with scattered nuclei, which is concave toward the outer surface and surrounds the inner surface of the lens; this system functions as a parabolic mirror which reflects to the outside light emitted by the luminous body and collected by the lens.

The organ is surrounded on the outside by a brownish-black pigment which extends to the lens on the outer surface, but only to half the lens on the inner surface. This pigment consists of fine granules;

oval nuclei are recognizable at points where the layer of pigment is thinner, so that this is apparently a separate layer of cells.

The reflector is passed radially by straight capillaries and thin nerves (Figure 12, *n.*) with elongate nuclei at various points. These capillaries and nerves are directed toward the luminous body. However, the blood supply is not as rich as in the previously described structures of the Enoploteuthidae and particularly the capillary network inside the luminous body is apparently much sparser.

A strand of connective tissue (*x.*) extends from the top of the lens and tapers strongly near the mirror. In front of this strand, i.e. toward the outside, the large chromatophores mentioned above (*chr.*) are situated; they are sometimes also present on the free outer surface of the lens.

The structure of the luminous organs of *C. hoylei* facilitates the understanding of the far more complicated conditions in other species of *Calliteuthis*. This applies particularly to the structure of the luminous body. The luminous body of *C. ocellata* and *C. reversa* forms a cup with several layers of luminous cells instead of a single layer. The luminous cells of *C. ocellata* resemble most closely those of *C. hoylei*, particularly the marginal cells which have a large, oval nucleus situated in the homogeneous proximal part of the cell, which stains intensively and is divided into fibers toward the pale distal part. The cells in the middle have the same structure, in that they consist generally of a light-colored part situated closer to the center and an intensively stained part that faces the reflector. All these cells extend radially toward the center of the cup and form numerous layers. The same structure is present in *C. reversa*, but the half of the cell facing the center is not divided into such fine fibers as in the other species (Figure 14). The cup-shaped luminous body with its multiple layers of luminous cells gives a confusing picture and may easily lead to erroneous interpretations, as will be shown later in connection with the description by Joubin.

162 The other differences are of minor importance and concern mainly the lens, the network of which consists of smaller and much more densely arranged cells than in *C. hoylei*. The mirror of *C. reversa* consists of small, undulate lamellae of connective tissue with scattered oval nuclei, as in the skin of other Cephalopoda where they cause the characteristic golden or metallic sheen. The layers of connective tissue which broadly cover the top of the lens between the mirror and outer skin consist of long, tubular cells which sometimes show rows of oval nuclei arranged behind each other. The intercellular substance develops a characteristic transverse striation between these long, sharply defined elements. The undulate transverse striations are usually widely separated, but sometimes densely arranged. Adjacent stripes are connected by delicate fibrils.

The luminous organs of the two species also differ in size: those of *C. ocellata* are 1.4 mm long, those of a large specimen of *C. reversa* 1.3 mm. Their longitudinal axis forms an acute angle with the surface of the body.

The description of Joubin generally agrees with our description of the different layers. I also made sections of the luminous organs of *Histioteuthis*, but the tissue was less well preserved than in *Calliteuthis*. At any rate, the luminous body of *Histioteuthis* apparently has a simpler structure than described by Joubin. Joubin (1893, p. 17) distinguishes 3 categories of cells: a basal layer of nerve cells, cells of connective tissue, and true luminous cells. He describes the latter as long, oval cells with a finely granulate content. Comparison with the luminous body of *C. hoylei* suggests that the bipolar nerve cells are actually spindle-shaped luminous cells; the cells of connective tissue apparently belong to capillaries with small nuclei.

Joubin (1894) reports that the lens cells of *Histioteuthis bonelliana* form two separate lenses. I could not find such a development in *Calliteuthis*. The drawing given by Joubin (*loc. cit.*, Figure 5, p. 11) shows that the two lenses are not sharply separated but that both lenses together form a hemi-

spherical surface. JOUBIN (1895, p. 6) described the lens of *Histiopsis* as a unified structure. JOUBIN gives the name "cône cristallin" to the central spindle-shaped cells which fill the luminous cup and which differ in form and coloration from the other cells of the lens.

I can add little to JOUBIN's description of the function of the different parts of the organs. If the organs are situated obliquely to the body surface, most of the light is emitted directly outward and only a small part is reflected by the mirror. In young specimens, however, especially in *C. hoylei*, the longitudinal axis of the organ is nearly parallel to the surface, and the mirror, which is situated obliquely
163 to the anterior surface of the preceding organ, functions more actively. As noted above (p. 126), there are chromatophores outside the mirror and partly also in front of the lens. These chromatophores are especially numerous and even arranged in 2 layers in the large specimen of *C. reversa*.

It can hardly be assumed that the expanded chromatophores absorb light. They probably function as color filters which change the quality of the light, i.e. its color, according to their state of contraction.

Mantle complex and inner organization

(Plate XX)

The mantle complex of a female *Histioteuthis* has already been described by WEISS (1886, pp. 83–85). However, it seems advisable to clarify some points which apparently escaped his attention. Moreover, the adult male was unknown until now.

Opening of the mantle cavity shows that the septum, which connects the mantle cavity with the abdominal wall, is displaced far posteriorly. It tears easily, which explains why it was overlooked until now. Its anterior margin is bordered by the mantle artery, which branches from the posterior aorta (Figure 5).

The posterior margin of the funnel is deeply indented between the two funnel cartilages, so that the anus is visible.

The strong funnel depressors (*mu. depr. inf.*) are attached to the dorsal margin of the cartilage on each side. They end in a point at the level of the base of the gills; a lamella of connective tissue connects them with the liver. Young specimens have a thin abdominal wall, through which the visceral complex is visible. The abdominal wall of adult specimens remains relatively thin but its pigmentation makes it difficult to distinguish the inner organs.

The **intestinal tract** is darkly pigmented. The esophagus extends dorsally above the liver and is colored dark in *Histioteuthis*. It opens in a long, sac-shaped stomach (Figure 5, *stom.*) which has a vivid purple color, tapers slightly and ends far from the posterior part of the mantle cavity. The much shorter caecum is situated anteriorly on the left side of the stomach, at the level of the gills. *Calliteuthis hoylei* has an ovoid caecum with the characteristic anterior spiral swelling from which dense lamellae extend through the whole interior. The pigmented mid-intestine begins between stomach and caecum; it ascends slightly to the left, passes behind the renal sacs, and finally emerges on the ventral side. The hind intestine is not sharply defined from the mid-intestine and opens between the two anal lips at the level of the funnel cartilage. The lateral anal appendages are asymmetrical and have a large dorsal lateral lobe (Figures 10, 11).

164 The large **liver** is surrounded by a tough capsule of connective tissue. On its posterior dorsal surface originate the bile ducts, which open into the caecum. The bile ducts are covered their whole

length by the dense pancreatic lobes, which form an anterior and a posterior mass. The ducts pass ventrally around the mid-intestine before opening jointly into the caecum.

The **ink sac** is tubular. It is situated ventrally on the liver behind the mid-intestine and opens into the hind intestine with a moderately long duct behind the anus.

Vascular system. The vena cava extends posteriorly on the right side near the mid-intestine. In front of the renal papillae and close to its entrance into the renal sac, it forms a long, spongy venous sac which widens posteriorly. Lateral to the venous sac are two ventral sacs (Figures 5, 6, *sacc. ven.*). They are 27 mm long in the large specimen of *Histioteuthis* and almost parallel, receiving posteriorly the abdominal vein, which is visible through the visceral sac. In the large male of *C. ocellata* these paired venous sacs are 10 mm long, crescent-shaped and extend obliquely to the branchial hearts.

The **branchial hearts** (*c. branch.*) are spherical in the young specimens, transversely oval in older specimens. They are 18 mm wide in the large *Histioteuthis* and form blunt triangles; those of *Calliteuthis ocellata* are only 7 mm wide.

The **appendage of the branchial heart** is not visible from the ventral side. It is situated dorsally on the branchial heart toward the midline; it is more oval in the large *Histioteuthis* and is 4 mm long.

The **gills** are always large and pyramidal in form; they are 55 mm long in *Histioteuthis* and 40 mm in *Calliteuthis*. The anterior end of the gills reaches to the lower third of the mantle cartilage. The gills and the branchial gland adhere closely to the mantle, and there is a short ligament only in the anterior part. It is characteristic for the gills of the Histioteuthidae that the inner and outer branchial lamellae do not differ much in length. The widest outer lamellae of *Histioteuthis* are 18 mm long and those of *Calliteuthis* 14 mm, and they are of about the same size as the widest inner lamellae. There are 40 lamellae on the outer side in *Histioteuthis*; there are 42 on the right and 40 on the left in *Calliteuthis*.

The branchial vein passes on the crest of the gill, receives the alternating efferent vessels of the branchial lamellae and expands on each side to form a thin-walled atrium, which opens in the heart. The **heart** has already been described by Weiss; it shows the normal structure of the Oegopsida. The heart of the large *Histioteuthis* measures 21 mm between the openings of the atria. The posterior aorta (*a. post.*), originates posteriorly in the heart; the mantle artery (*a. pall.*) branches off at the margin of the septum and then divides into the two fin arteries (*a. pinn.*) at the posterior end of the body.

The **renal sac** has no median septum. It opens in a chimney-shaped renal papilla (*ur.*) in *Cal-*
165 *liteuthis* and *Histioteuthis*. The inner opening of the renal sac is situated behind the renal papilla; it extends like a funnel toward the body cavity, close behind the outer papilla.

Genital organs

Our knowledge on the genitalia of the Histioteuthidae was incomplete until recently because adult males were not known. I was therefore pleasantly surprised to find that a large specimen collected by Doflein in Sagami Bay is a mature male of *Calliteuthis ocellata*.

Opening of the mantle cavity showed a very strange character: *Calliteuthis* **has double male genital ducts which open in 2 spermatophore sacs**. They are 10 cm long, cover the whole visceral sac and extend from the posterior end of the body to near the funnel (Figure 7).

The double male ducts are unique not only in the Cephalopoda but also among all the higher molluscs.

Only *Nautilus* shows an indication of paired male genital ducts inasmuch, that is, as the pear-shaped vesicle which opens in the mantle cavity at the base of the left lower gill is interpreted as a

rudimentary left gonoduct. Brock states that the genus *Tremoctopus* (*Ocythoë*) has a double vas deferens which opens in the single left terminal part of the gonoduct. This is not correct, as shown by Marchand (1907) in his study of the male genitalia of Cephalopoda.

Closer examination of the genitalia of *Calliteuthis* shows that the testis (*test.*) forms a flat, long band which consists of a dorsal and a ventral lobe. These lobes are fused on the left side, surrounding the chocolate-brown stomach anteriorly. The testis is attached by a light-brownish ligament which extends to the dorsal wall of the stomach, slightly on the left side. The dorsal lobe of the testis extends farther anteriorly than the ventral lobe, ending in two tips at the posterior wall of the liver; the ventral lobe extends farther posteriorly and bears some deep grooves which divide it into secondary lobes, as on the dorsal lobe.

Two vasa deferentia (*v. def. s.*, *v. def. d.*) open ventrally together in the body cavity near the testis. Both ducts form an angle; the left duct extends slightly further posteriorly than the right. Both vasa deferentia pass dorsal to the other genital ducts and open in the very large first parts of the seminal vesicle (*ves. sem. 1*). The left part of the vesicle is 31 mm long; both parts consist of a smaller anterior and a larger posterior part, both with a spongy structure. The first part opens in the sharply defined
166 second part (*ves. sem. 2*), which is narrower on the right side and more ovoid on the left side. The 2nd part bears posteriorly an *S*-shaped swelling which leads into the 3rd part. This (*ves. sem. 3*) is more distinctly divided into 3 parts than in other Oegopsida: it consists of a thick posterior part, a middle part which is curved anteriorly and a long, thin anterior part. This narrow duct receives on each side the relatively short, sac-shaped prostate (*prost.*) which is longitudinally folded. The wide caecum of the prostate (*app. prost.*) is situated at this point. The third part of the seminal vesicle continues in the vas efferens, which forms a sharp bend at the base of the caecum of the prostate and forms a large caecum, the function of which is unknown. The vas efferens then ascends posteriorly and opens on each side in the spermatophore pocket (*b. sperm.*).

From the constriction of the 3rd part of the seminal vesicle extends on each side a thin duct which I named "ciliated canal" (*c. cil.*). In *Calliteuthis*, both ciliated canals are free and visible with the naked eye as whitish ducts which open by way of ciliated funnels (*inf.*) near the median ventral plane. The opening of the left ciliated canal is situated far posterior to that on the right side.

The spermatophore sacs are unusually long in the mature specimen. They almost reach the apex of the testis posteriorly and their openings project far into the funnel on each side. The funnel has to be opened and folded aside to see these openings. The opening of the right spermatophore sac forms a loop posteriorly and a thick cluster of spermatophores is attached near the opening on each side. Both sacs (Needham's sacs) were filled with spermatophores.

The two genital ducts are not exactly symmetrical. The very large seminal vesicle extends further anteriorly on the right side than on the left, and the different parts of the vesicle are also markedly asymmetrical, as shown in the figure.

The presence of a double male genital duct in *Calliteuthis* induced me to find out whether a similar condition exists in *Histioteuthis*. The answer is negative: like all other Oegopsida, *Histioteuthis* has only a left genital duct, which closely resembles that of *Calliteuthis*. The seminal vesicle also has a large first part, followed by a sharply defined 2nd and 3rd part; the latter narrows into a long duct and the opening of the ciliated canal is situated at its base.

The spermatophore sac is also very long; in the large male, it has an *S*-shaped curvature at the level of the base of the gills. It was also filled with spermatophores.

I could not find a rudiment of a right genital duct. There was no trace of such a rudiment near the
167 base of the gills, where the male gonoduct begins to develop in immature Oegopsida.

I examined the **spermatophores** of *Calliteuthis ocellata.* The terminal filaments of the spermatophores are situated in the openings of the two spermatophore sacs, as shown in Figure 7. They are 7–8.5 mm long (excluding the filament) and otherwise show the characteristics of the spermatophores of the Oegopsida. Their delicate envelope ("étui" in the terminology of Rakovitza and Marchand) contains the sperm tube (Figure 8, *sp.*) and the ejaculatory tube (*proj.*), which opens on the "oral pole" (*or.*) near the filament (*fil.*). The sperm tube is about half as long as the spermatophore; its outer surface bears narrow spiral lines caused by the corkscrew-like gliding movement through the seminal vesicle. The sperm tube is situated on a long adhesive pad (*glut.*) which is surrounded by the delicate distal end of the ejaculatory tube (*proj.*). The walls of the latter thicken proximally and consist of several layers which constrict the lumen to a narrow canal (Figure 9, *proj.*). After the posteriorly directed loop, the ejaculatory tube opens in a fine pore (*or.*) where the eversion takes place during the discharge. This is caused mainly by the pressure of a secretion (Figure 9, *coll.*) which fills the space between the envelope and the two tubes.

Hectocotyli

The paired genital ducts are not the only exceptional character of *Calliteuthis.* It also **has two hectocotylized arms—the dorsal arms**. They are 26 cm long and bear proximally 23 pairs of normal suckers on the right arm and 21 pairs on the left arm. The distal part of each hectocotylus bears 58–61 pairs of suckers which become gradually smaller toward the apex. These suckers have stalks which are contiguous with those of the opposite row and resemble palisades. The suckers alternate regularly with those of the other side, forming a groove on the inner surface of the arms which probably serves for the reception of the spermatophores.

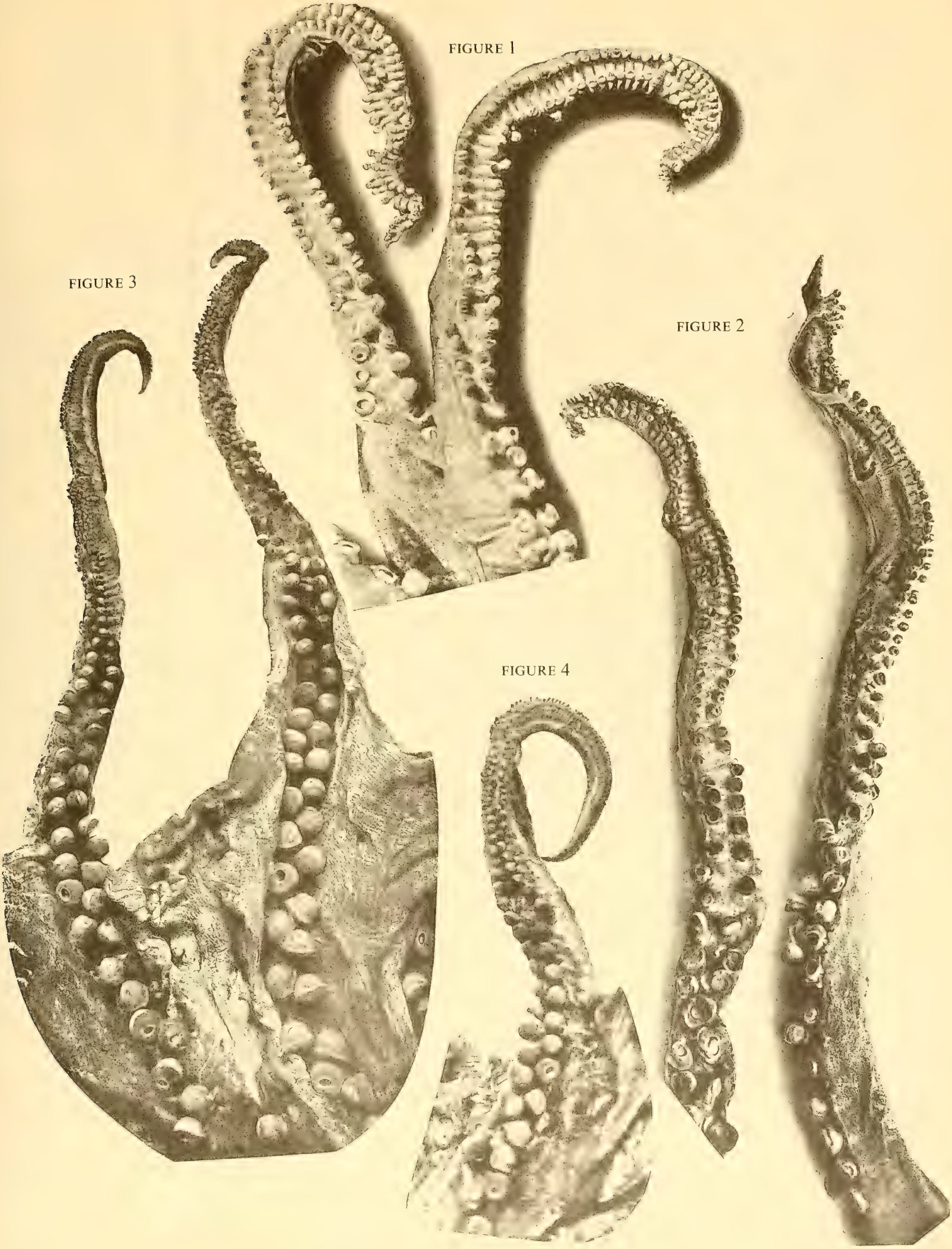
The **protective membranes** extend at half the height of the stalks and are fused with them. Text-plate 1 illustrates the transformation of the distal part of the arm and the difference between proximal and distal suckers.

After I had found this unique transformation of both dorsal arms into hectocotyli in *Calliteuthis*, I examined *Histioteuthis* for analogous formations. To my surprise, a large specimen of *Histioteuthis* which I purchased from the Brothers Gal, dealers in specimens in Nice, proved to be a mature male.
168 This is probably the largest specimen of *Histioteuthis* known. It is 585 mm long and has a dorsal mantle length of 165 mm. Examination showed that **both dorsal arms of the sexually mature male** ***Histioteuthis*** **are also hectocotylized**, as in *Calliteuthis* (Plate XXI). The arms are 33 cm long and, like the other arms, they bear the apical glandular swelling described by Verrill, which is 47 mm long.

The hectocotylization consists in a development of densely arranged suckers at the distal end of the arm. They are arranged more or less distinctly in 4 rows, instead of the biserial pattern in *Calliteuthis.* The suckers are situated on stalks which form a palisade and border on a groove which probably serves for the reception of the spermatophores.

As these specimens of *Calliteuthis* and *Histioteuthis* are the largest specimens which have been examined, I cannot decide whether the unusually large suckers on all arms are a secondary sexual character. This applies particularly to the normal proximal suckers of the hectocotyli, which are 7 mm wide in *Calliteuthis* and 8 mm in *Histioteuthis.* The suckers of the ventral arms are much smaller, only 2 mm in *Calliteuthis.* Females of *Histioteuthis* which had a mantle length of only 105 mm had much smaller suckers.

We mentioned above the glandular pads which form a ring around the opening of the suckers



TEXT PLATE 1

FIGURES 1 and 2. Hectocotylized dorsal arms of *Calliteuthis ocellata* OWEN. FIGURES 3 and 4. Same of *Histioteuthis rüpellii* VÉR.

in *Histioteuthis* and *Calliteuthis*. It is not known whether these pads are present only in the male.

The presence of two hectocotyli and double male genital ducts is certainly an indication of ancient conditions. The symmetrical genital ducts can be considered as a primary condition, reflected in the development of two copulatory arms. The latter condition is the more conservative, because the right duct has disappeared in *Histioteuthis* without a reduction of one of the two hectocotyli.

The above data suggest that primary conditions have persisted in the Histioteuthidae; but it would not be justified to consider them as the most primitive family of Oegopsida. Such characters as the 7- or 6-radiate structure of the buccal funnel do not suggest primitive conditions. The formation of 8 points on the buccal funnel is a primary character, in my opinion, which occurs only in the Enoploteuthidae, and especially in the genus *Thaumatolampas*, which also fits in with the simple radula. For the present, it can only be said that some primitive structural conditions have been retained in the different families of Oegopsida, except in the highly specialized Cranchiidae.

It is easier to establish the relationships of *Calliteuthis* and *Histioteuthis*. *Calliteuthis* is the more
169 primitive form because it has double genital ducts and its structure is recapitulated in the development of *Histioteuthis*. In the young *Histioteuthis* described as *Histiopsis*, the membrane ("sail") is not yet developed and closely resembles the genus *Calliteuthis*.

SYSTEMATICS

Histioteuthidae

Deep-sea Cephalopoda with gelatinous body; mantle goblet-shaped; fins of medium size, with indented posterior margin, projecting beyond the posterior end of the body. Funnel medium-sized, with a valve; funnel cartilage slightly curved, with a broad, deep, longitudinal groove; mantle cartilage wide, strongly projecting, tapering anteriorly. Head plump and wide. Eyes very large, spherical or conical; sinus of eye weakly indicated. Transverse grooves of neck projecting, ridgelike; olfactory tubercle situated on a low fold. Arms strongly developed, with biserial suckers, small swimming membranes and large protective membranes which may form a large membrane ("sail") between the dorsal and lateral arms; base of arms with outer membranes in the adult animal. Tentacles thick, with three-edged stalk and widened club the apex of which is curved dorsally like a hook; suckers of tentacles forming 5–8 rows in proximal hand part, 4 or fewer rows in the distal hand part; proximal suckers of median dorsal rows enlarged; adhesive apparatus of carpal part consisting of a dorsal marginal row of alternating suckers and knobs which pass to the ventral side on the stalk and form a long marginal row with two knobs alternating with two suckers. Buccal membrane with 7, rarely 6, pillars. Gladius with broad vane, without cone. Body usually of vivid coloration and with numerous ventral luminous organs; outer sides of arms with luminous organs in longitudinal rows which are more numerous on the ventral arms; right eye surrounded by numerous luminous organs, left eye by only a few organs; all luminous organs of similar structure, with reflector, pigmented sheath, lens and a mirror situated in front of the organ. Both dorsal arms of male hectocotylized.

The Histioteuthidae contain two genera, the differences of which are given in the following diagnosis:

Arms free, connected by membranes only at the base. Eyes conical. Hectocotylized dorsal
170 arms with biserial suckers in the distal half, situated on stalks which form a palisade. Buccal membrane with 7 pillars. Male genital ducts double. *Calliteuthis*

Arms, except tentacles and ventral arms, connected by a membrane formed by the widened protective membranes. Eyes spherical. Hectocotylized dorsal arms with suckers in 4 rows in the distal half. Buccal membrane with 7 pillars in the young stages and 6 pillars in the adults. Male genital ducts single.

Histioteuthis

Calliteuthis VERRILL, 1880

The genera *Stigmatoteuthis* and *Meleagroteuthis*, established by PFEFFER (1900), are so closely related to *Calliteuthis* VERRILL that I consider them as subgenera of *Calliteuthis*. The characters used by PFEFFER—the arrangement of the luminous organs, the supplementary chitinization of the suckers on the tentacles and the presence of tubercles on the arms and mantle—are specific characters which do not justify the establishment of new genera. I prefer, therefore, to place all these closely related species in the genus *Calliteuthis*. The following table shows the main differences between the species of *Calliteuthis*.

Luminous organs arranged in 3 rows on the ventral arms, in one row on the other arms (Subgenus *Stigmatoteuthis*)	Suckers on arms with weak teeth — *C. hoylei* OWEN
	Suckers on arms with crenelated indentations — *C. ocellata* OWEN
Luminous organs arranged in 3 rows on the ventral arms, in 2 rows on the other arms	Suckers on arms and tentacles without teeth — *C. reversa* VERRILL
Luminous organs arranged in 8 rows on the ventral arms, in 1–4 rows on the other arms (Subgenus *Meleagroteuthis*)	Dorsal midline of mantle and outer sides of dorsal and lateral arms with one row of cartilaginous tubercles. First and 2nd arms with 3 rows, 3rd arms with 4 rows of luminous organs — *C. meleagroteuthis* PFEFFER (= *M. hoylei* PFEFFER)
	Cartilaginous tubercles absent. First arms with one row of luminous organs, 2nd arms with 2 rows, 3rd arms with 3 rows — C. asteroessa n. sp.

Calliteuthis hoylei GOODR.

(Plate XVIII, Figure 1; Plate XIX, Figure 6; Plate XX, Figures 1, 2, 5, 10, 12)

Histiopsis hoylei GOODRICH, 1896, p. 15, Plate 4, Figures 62–71.
Histiopsis hoylei HOYLE, 1897, *Cat. Rec. Ceph. Suppl.*, p. 11 (373).
Stigmatoteuthis hoylei PFEFFER, 1900, p. 170.

171 **Locality**: Station 235, Indian South Equatorial Current near the Amirante Islands; 4°34′ S, 53°42′ E. Vertical net to 2,000 m—One female.

C. hoylei was discovered near the Andaman Islands. Goodrich placed it in the genus *Histiopsis*. I agree with Pfeffer, who considers *Histiopsis* as a juvenile stage of *Histioteuthis*. However, I place this species in *Calliteuthis*, while Pfeffer established the new genus *Stigmatoteuthis*, the only distinct difference of which from the other species of *Calliteuthis* is in the arrangement of the luminous organs.

I have a well-preserved specimen which we caught with a deepwater net at Station 235 near the Amirante Islands. Only a few remarks might be added to the detailed description of Goodrich.

Our specimen is almost as large as that described by Goodrich. However, the head is slightly wider than the mantle and the relatively small fins project only little beyond the posterior end of the body. As in all Histioteuthidae, the arms differ little in length. The 3rd and 2nd arms are 25 mm long, the ventral arms 22 mm, and the dorsal arms 21 mm. The body is 45 mm long, including the ventral arms. All arms have 4 edges and are vividly pigmented on the outside. The protective membranes are well developed but taper toward the tip and the base, so that they do not form a "sail" at the base. Outer membranes are present at the base of all arms; the swimming membranes are weak and keel-shaped and are present only in the distal half of the 3rd arms.

Both tentacles are well preserved. They are thick, with 3 edges, and end in a slender, slightly widened club (Plate XIX, Figure 6). The suckers of the hand part are arranged in 5 to 6 indistinct rows in the proximal part and gradually assume the normal arrangement in 4 rows in the distal part. The two median dorsal rows of the proximal part contain 4–5 larger suckers, and the marginal suckers are very small. Narrow protective membranes are distinct, and a keel-shaped swimming membrane occupies the space between the broader part and the tip of the club, which is slightly curved dorsally.

The carpal part of the club consists of about 5 dorsal suckers, and about 3 adhesive knobs between them. It continues on the stalk in a long row of 6 suckers which is directed toward the ventral side, where 2 suckers alternate with 2 knobs.

As already described by Goodrich, the suckers on the club bear numerous fine marginal denticles. His figure shows that these denticles cover the whole margin uniformly; I found about 20 denticles only in the dorsal half; the ventral half is smooth.

The **suckers** on the arms also have fine denticles in the dorsal half, 7 in my specimen.

172 The **buccal funnel** consists of 7 pillars which end in 7 points. From the pillars between the dorsal arms extend two fine membranes of attachment to the dorsal side of the arms. The other pillars have one membrane each; the 2nd and 4th arms are attached dorsally, the 3rd arms ventrally.

The left eye (Plate XX, Figure 1), of which I made sections (p. 118), is ovoid because it is longer than wide. This is the first indication of transformation into a telescopic eye, which will probably become more distinct in the fully grown animal. The eye is 8 mm long and 6 mm wide. This lengthening of the main axis causes the steep position of the ciliary region and the iris. Clearing in oil of cloves shows the reddish brown pigmented envelope, which extends to the edge of the iris. The optic ganglion (*g. opt.*) is visible on the inner surface; it is 3.5 mm wide and 1 mm thick and is situated below the band-like, crinkled white body (*c. alb.*).

Our specimen has a vivid purple coloration with a brownish tone; only the fins, funnel and tentacles are paler. The sucker-bearing inner sides of the arms are intensively reddish brown, especially in the proximal parts near the buccal funnel.

The luminous organs are prominent and present not only on the ventral side but, in smaller number, also on the dorsal side. There are 12 small, almost symmetrically arranged organs on the dorsal side of the mantle, two of them in the midline of the gladius. Most organs are situated on the ventral side, where they form oblique rows. The organs are especially dense on the ventral margin of the mantle, where the indentation between the two corners bears 10 organs. The right eye is surrounded by a dense

circle of organs, but there are only 2–3 indistinct organs around the left eye. The ventral arms bear 3 rows of organs except at the tip, where there are only 2 rows. The other arms bear only one row of organs on the ventral margin.

Mantle complex
(Plate XX, Figure 5)

Opening of the mantle cavity shows the long funnel cartilages which widen posteriorly around the deeply incised funnel. A deep depression is situated between the cartilages. The opposite cartilages on the mantle project distinctly, like ridges. If the dorsal mantle corner is further bent laterally, it appears that the neck cartilage is only slightly broader anteriorly (Plate XX, Figure 2). A groove with raised margins extends in the middle of the neck cartilage. The opposite mantle cartilage is lanceolate and extends with its tapering end to the mantle margin. A ridge in the middle of this cartilage fits into the groove of the neck cartilage.

173 The two strong funnel depressors (*mu. depr. inf.*) are attached at the dorsal margin of the funnel cartilage and extend obliquely to the base of the gills. The chocolate-brown hind intestine is situated between them and opens in the light-colored anus, which has two lips. The anal appendages (Figure 10) have a dorsal lateral lobe. The stomach is also deep chocolate-brown and the colorless caecum is visible at the base of the left gill.

The vena cava passes on the right side near the hind intestine and opens in an oblong venous sac; the rounded renal papillae (*ur.*) are visible lateral to it. Then follow posteriorly two symmetrically situated venous sacs (*sacc. ven.*) which open in the spherical branchial hearts from which the short branchial arteries originate. The gills are narrow and reach to near the mantle cartilage. On their ventral edge passes the branchial vein, which is not visible dorsal to the symmetrical venous sacs. Also visible through the thin-walled visceral sac are the two abdominal veins (*v. abd.*) and the single posterior aorta (*a. post.*). The posterior aorta from which the mantle artery (*a. pall.*) branches is visible on the delicate septum which extends to the mantle. The aorta then branches into the two arteries of the fins (*a. pinn.*).

The specimen is a young female; the relatively long ovary is visible dorsal to the stomach. The genital ducts, however, are still little developed. The opening of the two oviducts (*od.*) is situated behind the base of the gills and there are 2 narrow light stripes which I consider as the "anlage" of the nidamental glands (*nid.*) on the abdominal wall at the level of the paired venous sacs.

Measurements

Dorsal length of mantle	15.5 mm
Maximal width of mantle	8.5 mm
Width of both fins	9 mm
Width of head	10 mm
Length of 1st arm	21 mm
Length of 2nd arm	25 mm
Length of 3rd arm	25 mm
Length of 4th arm	22 mm
Total length to tip of 4th arms	45 mm

Calliteuthis reversa Verrill

(Plate XVIII, Figures 2–4; Plate XIX, Figure 5; Plate XX, Figures 3, 4, 6, 11, 13, 14)

Calliteuthis reversa Verrill, 1880, *Amer. Journ. Sci.*, Vol. XX, p. 393.
Calliteuthis reversa Verrill, 1881, *N. Amer. Ceph.*, p. 295, Plate 46, Figure 1.
Calliteuthis reversa Verrill, 1884, *Sec. Catal.*, p. 243.
Calliteuthis reversa Hoyle, 1886, *Challenger Ceph.*, p. 183, Plate XXXIII, Figures 12–15.
Calliteuthis reversa Goodrich, 1896, *Ceph. Calcutta Mus.*, p. 16, Andaman Islands.
174 *Calliteuthis reversa* Pfeffer, 1900, p. 170.
Calliteuthis reversa Joubin, 1900, *Camp. Sc. Pr. Monaco*, p. 96, Plate XII, Figures 4–5, Mediterranean.
Calliteuthis reversa Hoyle, 1904, *Albatross Ceph.*, p. 42., Atlantic, Cape Mala.

Locality: Station 223, Indian Countercurrent, 6°19′S, 73°18′E. Vertical net to 1,900 m—One young female.

Calliteuthis reversa was described in detail by Verrill. We caught this widely distributed species with a deepwater net at Station 223 near the Chagos Archipelago in the Indian Ocean. Although Verrill's description is excellent, it is of interest to describe a juvenile specimen, especially because some details have been only superficially described. I also have a well-preserved arm apparatus of an adult specimen caught by the German South Polar Expedition.

The young specimen has a completely gelatinous body. It had a magnificent red coloration in life, which is reproduced in watercolor in Plate XVIII. Furthermore, luminous organs are present; their arrangement and structure will be discussed at the end of the description.

The specimen is 41 mm long, the mantle 17 mm, and the arms 15 mm long. The dorsal mantle corner is blunt, almost flat, while the ventral corners project more distinctly. The mantle is narrow, goblet-shaped; the fins are pale, their dorsal attachments diverge broadly and their heart-shaped indented posterior margin projects only little beyond the end of the body. The funnel is relatively small and tapers anteriorly. The head is plump and markedly wider than the mantle. This is mainly due to the relatively large eyes, the background of which was a deep purple red in the live animal. Neck folds are not recognizable, but the small, stalked olfactory tubercle is distinct.

The arms are moderately long. They are of about equal length—14–15 mm. They have four edges, and are red on the outer side and paler on the lateral and inner surface. There are 16 pairs of suckers on the 1st arms, 15 on the 2nd arms, 16 on the 3rd arms, and 18 pairs on the 4th arms. The rings of the suckers are completely smooth, without indentations.

The **tentacles** are relatively short and thick. Their three-edged stalk widens distally to form the club, the tip of which is sharply curved dorsally, like a chamois horn. In its concavity extends the swimming membrane, which is also displaced dorsally (Plate XIX, Figure 5). The club of *C. reversa* is wider than that of *C. hoylei* and *C. asteroessa*, but its hand part also bears not more than 7 oblique proximal rows of suckers. The median dorsal rows contain also 4–5 enlarged suckers. The suckers gradually assume the arrangement in 4 rows in the distal hand part. The adhesive apparatus consists of a dorsal row in which 5 suckers alternate regularly with knobs. Then follow alternating pairs of suckers and knobs
175 which pass to the ventral side of the stalk. The tentacle club was first described by Hoyle, because it was lost in Verril's specimen.

The arm apparatus of the adult has also lost the tentacle clubs, but the arms are well preserved. They are respectively 80, 92, 87 and 74 mm long. The 2nd arms are thus the longest, but the arms

differ little in length (formula: 2, 3, 1, 4). The wide protective membranes form a weak sail-shaped membrane at the base of the arms; the outer membranes are thin and inconspicuous. A thin, keel-shaped swimming membrane is present on the distal half of the 1st, 2nd and 3rd arms, being somewhat larger only on the 3rd arms. The ventral arms have no swimming membrane and bear only small suckers, which are slightly more densely arranged.

The buccal funnel and attachments of the arms of the young specimen are shown in Plate XX, Figure 3. The buccal funnel has 7 semitransparent buccal pillars which end in 7 points and which clearly reveal the central nerve extending through them. A forked attachment extends from the single dorsal pillar to the dorsal arms, while the other pillars have a single attachment to the base of the arms. The 1st, 2nd and 4th arms are attached dorsally, the 3rd arms ventrally. The tentacle is attached ventrally by a fine muscular ligament. The buccal funnel is situated like a roof on the united bases of the arms, so that there are 6 pori aquiferi.

The distribution of the **luminous organs** of *C. reversa* was described by PFEFFER as follows: "Dorsal and dorsolateral arms with one row of large luminous spots and one row of small spots; ventrolateral and ventral arms with three rows of large luminous spots."

Care has to be taken in the interpretation of the arrangement of luminous organs as specific and generic characters, as a comparison of the young specimen with the arm apparatus of the adult specimen shows. The proximal half of the ventral arms of the adult bears 3 rows of large organs, but only 2 rows distally. There is, however, an additional row of small, indistinct organs on the dorsal margin of both arms which extends slightly beyond the proximal half. The 3rd arms have only 2 rows of organs, a ventral row with large organs and a dorsal row with small organs. This is also the case on the 2nd and 1st arms, as PFEFFER noted. In the young specimen, the organs on the arms are still little developed; the 1st and 2nd arms have only one row of ventral organs. The 3rd arms have two rows, the ventral arms have 3 rows which also pass into two rows towards the tip. As shown in the figures, the ventral side of mantle and head bears crossing oblique rows of luminous organs; the dorsal side of the mantle and
176 head has only a few small organs. As in all species of *Callitheuthis* examined, the lid margin of the right eye bears numerous luminous organs (18 in my specimen); the left eyelid has no luminous organs, but 3 such organs are present some distance from it.

The **inner organization** on the whole resembles that of *C. hoylei.* Figure 6 of Plate XX shows the mantle complex of a young female the two oviducts of which are concealed behind the base of the gills, and the nidamental glands (*nid.*) are visible as whitish stripes at the level of the two venous sacs (*sacc. ven.*).

Measurements of *C. reversa* juv.

Total length	41 mm
Dorsal length of mantle	17 mm
Width of mantle margin	9 mm
Width of head	12.5 mm
Transverse width of fin	9.5 mm
Length of 1st arms	14 mm
Length of 2nd arms	15 mm
Length of 4th arms	14.5 mm

Measurements of the large *Histioteuthis rüppellii* (male). Plate XXI

Total length	585 mm
Dorsal length of mantle	165 mm
Transverse width of both fins	126 mm
Dorsal length of fin	88 mm
Width of head	100 mm
Length of head (from dorsal mantle margin to base of 1st arms)	90 mm
Length of 1st arms (hectocotyli)	330 mm
Length of 2nd arms	320 mm
Length of 3rd arms	325 mm
Length of 4th arms	270 mm
Length of tentacles	340 mm

Postembryonic development of *Histioteuthis* and *Calliteuthis*

a) *Histioteuthis*

(Plate XVIII, Figures 6, 7; Plate XIX, Figures 1–4)

Our knowledge on the postembryonic development of *Histioteuthis* is based mainly on the view that *Histiopsis* Hoyle is a juvenile form of this genus (this will be discussed in detail below). I intend to describe here some larval forms which undoubtedly belong to the developmental cycle of *Histioteuthis*. They are much smaller than *Histiopsis*, but show some characters which leave no doubt that they belong to *Histioteuthis*. One of the larvae was caught at Station 73, two others were caught in the Mediterranean, near Messina and Villefranche, i.e. the very areas from which previous specimens
177 of *Histioteuthis* have come. The largest specimen is the one from Messina (Plate XIX, Figure 1); it will be described first to show that these larvae belong to *Histioteuthis*.

This larva is 17 mm long and has a dorsal mantle length of 8 mm. The mantle is goblet-shaped, with a slightly rounded posterior end and somewhat projecting ventral corners. The fins are large and their dorsal bases are situated so close together that the fin has the form of a disc 8 mm wide, attached obliquely at the posterior end. The fins project 2 mm beyond the posterior end of the body and are united in front of the tip. A median groove indicates the posterior boundary between the fins. The large fins, their closely approximated bases and the fact that they project markedly beyond the posterior end of the body are so characteristic, that they strongly suggest that the larva belongs to *Histioteuthis*.

The head is 5 mm wide. The transverse and longitudinal folds of the neck form small, indistinct swellings, but the olfactory tubercles are distinct, though covered by the ventral corners of the mantle. The eyes are large, with a wide opening and an indistinctly developed sinus. The funnel projects to the level of the lower margin of the eyes and has two adductors. The arms are well developed but there is no sail-like membrane; the 2nd arms are the longest. The protective membranes, which later form the sail membrane, comprise only small, undulate folds along the rows of suckers. The outer membranes at the base of the arms, too, are only weakly indicated.

The tentacles are relatively short and thick but they are longer than the other arms. Their three-edged stalks bear large chromatophores in one row on the outer side. The club (Figure 2) is only slightly widened and shows a keel-shaped distal swimming membrane. The proximal hand part consists

of small suckers of about equal size, arranged more or less distinctly in oblique rows of 6–8 suckers; they pass gradually into rows of 4 suckers in the distal part.

The carpal part consists of about 5 suckers of the dorsal marginal row and there are indistinct knobs between them. They are adjoined by paired suckers which continue ventrally on the stalk and alternate with indistinct knobs.

The buccal membrane forms only a narrow membrane around the buccal cone, but already shows distinctly the 7 buccal pillars and their attachments.

The luminous organs are distinct, like whitish pearls. They form crossing oblique rows on the ventral side of the mantle and curves on the ventral side of the head which are nearly parallel to the eye margin. The organs around the eyes are also distinct and show the asymmetrical arrangement characteristic for the adult *Histioteuthis*. The margin of the left eye has a semicircle of only 7 organs;
178 the right eye is completely surrounded by 17 organs. There is only a small gap dorsally, before which the 18th organ is situated; it is not certain that it belongs to the same type as the other 17. Around the right eye of the adult *Histioteuthis*, too, there are 17 luminous organs. The organs continue in 3 rows on the ventral arms, of which the median row continues to the tip. The 2nd and 3rd arms have one row of organs on the ventral margin, while the dorsal arms are without luminous organs, except for a single organ at their ventral base.

Regarding the structure of the luminous organs, sections of the organs of the mantle show the following details. The youngest organs, which are hardly visible at the margin of the mantle, consist of oval clusters of cells in the cutis, below the epidermis. A relationship to epidermal cells, which could suggest the ectodermal origin of the organs, is not recognizable. Comparison with older stages shows that the luminous cells develop from these clusters of cells. In the larger organs, the cluster of cells is already surrounded by cells of connective tissue that develop into the characteristic squamous cells. A pigmented cup is absent also in the fully developed organs. The association with chromatophores is evident, because a chromatophore is situated constantly behind each ventral organ. As the organs of *Calliteuthis* and *Histioteuthis* are very similar, it is difficult to decide in these young stages to which genus they belong.

The larva has a tough, fleshy body.

A smaller larva which I obtained from Professor Woltereck resembles the above larva in its characteristic form. It was caught in 1903 in deep water near Villefranche. It is 11 mm long, with a dorsal mantle length of 5 mm and head width of 3 mm. The fins project beyond the goblet-shaped mantle and are fused posteriorly, so that there is only an indentation between them (Plate XVIII, Figures 6, 7). The fins are relatively large, both fins together being 5 mm wide. Otherwise, the larva closely resembles the stage described above. The characteristic form is shown in the illustrations. The main differences are in the luminous organs, which appear as whitish dots on the ventral side of the head but are absent on the mantle, around the eyes and on the arms. The pigmentation is vivid and shows a certain symmetry in the arrangement of the chromatophores. The stalks of the tentacles bear a regular row of broad chromatophores.

179 Another larva, caught at Station 73 in the Benguela Current, is very similar (Plate XIX, Figure 3). It is slightly smaller, 9 mm long, with a dorsal mantle length of 4.5 mm and head width of 2.5 mm. It also has large fins which are together 4 mm wide and project beyond the posterior end.

The luminous organs are even less developed than in the former larva. Several whitish tubercles in oblique rows are visible on the ventral surface of the head. The attachments of the arms, the 7-radiate buccal funnel and the regularly fluted inner lip of the mouth are distinct.

The club (Plate XIX, Figure 4) is relatively plump; otherwise it resembles that of the former specimen.

The hand part is densely covered with small suckers of equal size, arranged in indistinct oblique rows of 7–8 suckers which gradually pass into rows of 4 suckers at the apex of the club. The rows of suckers of the hand part become looser toward the stalk and it is difficult to say where the carpal part begins, especially because knobs are absent and the paired suckers of the stalk have not yet been displaced to the ventral margin of the stalk.

This larva is vividly pigmented, except for the fins. The outer side of the club, tentacle stalk and arms are also intensively colored.

b) *Calliteuthis*

(Plate XVIII, Figure 5)

One larva caught with a vertical net at a depth of 2,000 m at Station 112 outside the Agulhas Bank differs markedly from the youngest larvae of *Histioteuthis* described above. It is of about the same size as the juvenile form of *Histioteuthis* from Station 73. Measurements: total length 9 mm, dorsal length of mantle 3.8 mm, width of head 2.5 mm. This specimen is more slender than the previously described larvae and also has relatively small fins which are together 2.5 mm wide and project only slightly beyond the posterior end.

The luminous organs are numerous and almost symmetrically arranged. They shine strongly on the ventral side of the head and less distinctly on the mantle, where 3 whitish "anlagen" are visible associated with chromatophores.

The club is much more slender than in the larvae of *Histioteuthis.* The hand part bears very small suckers which form loose oblique rows of about 6 suckers. The stalk bears two pairs of suckers, of which the proximal pair is situated on the ventral edge.

In view of these conditions it appears uncertain that this larva does indeed belong to *Histioteuthis*; it is probably more correct to place it in the genus *Calliteuthis.*

180 Lo Bianco (1903, p. 172, Plate 8, Figure 22) described a larva collected by Krupp in deep water in the Gulf of Naples. This larva, which is 8 mm long, was determined by Jatta as a juvenile form of *Histioteuthis* (*Histiopsis atlantica* Hoyle). As the fins, club or luminous organs have not been described, it is difficult to decide whether the larva belongs to *Histioteuthis* or *Calliteuthis.*

4. Family **Onychoteuthidae** GRAY, 1849

Teleoteuthis VERRILL, 1882

Postembryonic development

(Plate XXII; Plate XXIII, Figures 11–14).

PFEFFER (1900, p. 156) wrote the following about the juvenile forms of *Teleoteuthis*: "The young animals have 4 rows of suckers on the tentacle club and have been described as the genus *Steenstrupiola* PFEFFER 1884; the suckers of the marginal rows are larger than those of the middle rows in *T. caribaea.*

"A very typical character which distinguishes young animals of this genus is a very large chromatophore which forms an oblong dark lateroventral spot at half the length of the fins."

Such young forms have been described also by JOUBIN (1900, p. 68; Plate X, Figure 14; Plate XV, Figures 14, 15). He described them as a new species, *T. jattai.* I do not agree with this, because these differences from the specimens described here are readily explainable as differences from the adults.

The young specimen described by JATTA (1896, p. 101; Plate XIII, Figures 35–41) as *T. caribaea* is a young *Abraliopsis*, as already stressed by PFEFFER (p. 157) (cf. p. 64).

1. *Teleoteuthis caribaea* LESUEUR, 1821. Larvae

A number of delicate larvae of *T. caribaea* were collected at the surface at Station 49 in the Atlantic South Equatorial Current, and I am describing some characters of interest for the comparative anatomy of the tentacle club.

The youngest stage (Plate XXII, Figures 1, 2) has a mantle length of 5 mm. The mantle is sac-shaped; it extends to half the level of the eyes and forms posteriorly a short tip, with two transversely oval fins. The chromatophores are symmetrically arranged; a row of dark chromatophores extends on the dorsum and on the outer side of the 1st and 2nd arms. There are 3 pairs of more strongly colored
181 chromatophores in front of the fins; more weakly colored chromatophores are visible in the layers of the cutis. The eyes are moderately large; the head is partly retracted in the mantle.

All arms are already present and slightly shorter than the club-shaped tentacles; their formula is 2, 3, 1, 4. The 1st arms are keeled and bear about 8 chromatophores and 10 distinct pairs of suckers. The 2nd arms bear 12 pairs of suckers and 8 chromatophores in the distal half. A keel (swimming membrane) is only weakly developed. The 3rd arms bear a distinct keel and 10 pairs of suckers; they have only 2 chromatophores distally. The 4th arms are small and bear 8 pairs of suckers and several very small suckers at the tip, like the other arms. Distinct protective membranes with muscular bridges are present on the 1st and 2nd and 3rd arms.

The tentacles (Plate XXIII, Figure 11) are short, plump, with suckers on the flat inner surface. There are 5 pairs of suckers in a zigzag row near the base (the later carpal part), followed by about 10

rows of quadriserial suckers (hand part). There is no keel, and the protective membranes are only indistinctly developed.

In a slightly older stage (Plate XXII, Figures 3 and 4), head and funnel project further from the mantle; almost all chromatophores were strongly contracted. The fins are larger, the arms are almost as long as the tentacles and bear distinct swimming membranes, which are especially distinct on the 3rd arms. The swimming membranes of the 4th arms extend at the base as outer membranes around the still short tentacles. The suckers have become more numerous, mainly on the 3rd arms, which bear about 15 pairs. The tentacles (Plate XXIII, Figure 12) bear 6 pairs of suckers in a zigzag row on the stalk. Then follows a row of 3 suckers, and the usual quadriserial rows of club suckers, of which the proximal rows include a number of slightly larger suckers at the margin. A keel which is slightly dorsally displaced is present at the distal end of the club.

This stage already shows the first indications of neck folds, particularly those that bear the olfactory tubercles.

Older stages show more distinct characters of the genus. Figures 5 and 6 show a larva with a mantle length of 10 mm and with edged arms. The swimming margins are weakly developed on the 1st, 2nd and 4th arms but well developed on the 3rd arms. The 1st arms bear 17 pairs of suckers, the 2nd arms about 20, the 3rd about 16 and the 4th about 15. Small suckers are present at the apex of the arms. Protective membranes are present everywhere, but are weakly developed.

The **tentacles** (Plate XXIII, Figure 13) have angular edges. The zigzag rows of paired suckers are
182 dense at the distal end of the stalk, so that the paired arrangement becomes indistinct. This suggests that they are going to form the carpal part, which consists here of 12 small, densely arranged suckers. The club contains the usual quadriserial rows of suckers, which pass proximally into a row of 3 and then into a row of 2 suckers. As already indicated in the younger stage, both outer rows of the club contain larger suckers but the difference is more distinct. There are 11 suckers on the ventral outer margin and about 9 larger suckers on the dorsal outer margin.

The **chromatophores** are arranged in two layers: dark superficial chromatophores, and lighter-colored chromatophores in the deeper layers. A row of brown chromatophores extends on the dorsum and on the outer surface of the arms.

In addition, 2 distinct dark chromatophores are situated near the base of the fins. These chromatophores, as noted by Pfeffer, are present already in the youngest stage.

The oldest of the young stages I have (Plate XXII, Figures 7, 8) already shows some characters of the adult *Teleoteuthis*. It has a dorsal mantle length of 15 mm and well-developed neck folds of which the middle fold is crescent-shaped and bears a low olfactory tubercle at the posterior margin. The arm formula is 2, 1, 3, 4. A well-developed keel is present on the 3rd arms, the other arms have weakly developed keels.

The tentacles (Plate XXIII, Figure 14) have angular-edged stalks and resemble the definitive condition. The club shows distinct protective margins and a wide dorsal keel. It consists of a carpal part and a hand part. As Pfeffer (1884, p. 17) noted for *Steenstrupiola atlantica*, the carpal part of the right tentacle bears 9 suckers, and 8 distinct knobs, that of the left tentacle 10 suckers and about 9 knobs. These are followed by a row of 3 smaller suckers and 3 rows of 4 larger suckers. Then follow 8 rows of 4 suckers, of which the median suckers have already begun or have completed their transformation into hooks. The distal end of the club bears an irregularly arranged group of suckers.

As this condition is preparatory to the definitive form of the club of *Teleoteuthis*, the corresponding characters of the youngest stages may be mentioned. The tentacle stalk of the young larvae bears 5–6 pairs of small suckers in a zigzag arrangement. These become gradually more densely arranged,

forming the carpal part, with 9–10 suckers, between which an equal number of knobs gradually develop. The tentacles of the youngest stages resemble those of the Histioteuthidae, Tracheloteuthidae and Cranchiidae in their zigzag arrangement of paired suckers on the stalk. These suckers are homologous with the distinct carpal part of the club of the Enoploteuthidae, Onychoteuthidae and other families. This explains the fact that the Oegopsida with suckers on the stalk of the tentacles have no clearly defined carpal part on the club, while those with a clearly differentiated carpal part have no suckers on the stalk.

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2. Youngest Stages of Onychoteuthidae
(Plate XXIII)

There is a group of larvae which certainly belong to the Onychoteuthidae. This is proved by the fact that the mantle cartilage of the older stages forms a simple ridge, fitting into the narrow longitudinal groove of the funnel cartilage which slightly tapers anteriorly. They differ from equally large larvae of Enoploteuthidae in a number of characters: the compact form, the relatively short arms and, mainly, the thick tentacles, which are hardly longer than the arms and may be mistaken for them.

The youngest specimen (Plate XXIII, Figures 1 and 2) is 2.3 mm long and has a dorsal mantle length of 1.7 mm. Its small, transversely oval fins do not project beyond the posterior end of the body; the mantle ends behind the eyes, so that the small funnel, which is curved downward, is exposed.

There are only 3 pairs of arms. Only further development shows that the ventral pair represents the later tentacles. This is also indicated by the small knobs at the base of the tentacles which represent the "anlagen" of the 3rd arms; there is no trace of the 4th arms. The larva thus has only two pairs of arms, the 1st and 2nd; the 3rd arms are only in the "anlage". The tentacles bear 4 pairs of suckers, the other arms only 3 pairs.

The chromatophores are sparse: 5 symmetrically arranged chromatophores on the ventral side of the mantle and 2 median chromatophores on the dorsal surface. Two chromatophores are also already present at the ventral base of the fins in this early stage. The head bears 2 dorsal and 2 ventral chromatophores at the base of the tentacles; each tentacle bears 2 chromatophores on the outer side, and the arms bear 1–2 chromatophores.

Figures 3 and 4 show a similar stage but it is slightly larger: it bears 4 or 5 pairs of suckers on the arms but shows no progress in the development of the 3rd arms. The tentacles bear 5 pairs of suckers and a few suckers at the tip which tend to form rows of 3 or 4.

The older stages illustrated in Figures 7 and 8 have longer tentacles, further developed 3rd arms and developing 4th arms in the form of small stumps. They have a dorsal mantle length of 3.3 mm. Between their transversely oval fins extends the gladius, which shines through and ends in a sharp point. The 1st and 2nd arms bear 5–6 pairs of suckers, and a few very small suckers at the tip. There are 5 pairs of alternating suckers on the tentacles and some distal suckers in oblique rows of 3 or 4. Comparison
184 with the suckers on the tentacles of the stages of *Teleoteuthis* described above shows that the paired suckers represent the carpal part, while the other suckers form the club.

The chromatophores are still sparse, but slightly more numerous on the outer side of the arms and tentacles. Especially distinct are the two chromatophores on the ventral side of the base of the fins.

The oldest specimen (Figures 9 and 10) is 5.5 mm long and has a dorsal mantle length of 3.7 mm. Its mantle is goblet-shaped and the fins are relatively small. Funnel and eyes are of medium size and are not covered by the mantle margin. All arms are present; the 3rd arms are barely half as long as the

2nd arms and the 4th arms are still very short and stumpy. The arm formula is 2, 3, 1, 4. The 1st arms bear about 5 pairs of suckers, the 2nd arms about 6 pairs, the 3rd arms only one pair. A small keel is recognizable on the 1st and 3rd arms.

The relatively short tentacles bear about 9 oblique rows of suckers. The 5 or 6 proximal rows consist of only 2 suckers, the other rows of 3 or 4 suckers. The club itself is still little developed in this stage, despite the advanced differentiation of the carpal part which apparently develops from the proximal pairs of suckers.

The chromatophores are still sparse, but more numerous than in the preceding stage. There are 4 very large chromatophores which occupy the whole dorsal side. There is also one chromatophore under the fins. The dorsal surface of the head bears 4 symmetrically arranged chromatophores, the tentacles 5, the 1st and 2nd arms only 2–3 chromatophores.

Comparison of the oldest of these larvae shows some resemblance to the previously described larvae of *Teleoteuthis*. I therefore assume that these larvae are young Onychoteuthidae, the postembryonic development of which can be described as follows:

1. Only the 1st and 2nd arms are present in the youngest larvae, the 3rd and 4th arms develop later.
2. The tentacles grow at first very slowly and closely resemble the other arms. Their differentiation begins with the formation of biserial suckers on the carpal part, while the club is little developed even in older stages.
3. The chromatophores are sparse and symmetrically arranged. Two ventral chromatophores are present at an early stage at the base of the fins; a dorsal row of chromatophores develops later along the gladius.

Another small larva (Figures 5, 6) probably also belongs to the Onychoteuthidae, though it has a slightly different form. It is plumper and the 3rd and 4th arms are already present as stump-shaped "an-
185 lagen" despite the shortness of the other arms. The 1st and 2nd arms bear 3 pairs of suckers and a single sucker at the base. The tentacles show a similar arrangement but the small suckers of the later club part are already present at the tip.

5. Family **Bathyteuthidae** PFEFFER

Ommastrephini subf. Ommastrephidae p. p. HOYLE, 1886, p. 36.
Bathyteuthidae PFEFFER, 1900, pp. 152, 171.
Bathyteuthidae HOYLE, 1909, p. 271.

PFEFFER (1900, p. 171) gives the following diagnosis of the family Bathyteuthidae, which he established for the genera *Ctenopteryx* and *Benthoteuthis* (*Bathyteuthis*):

> "Funnel cartilage simple, with a narrow groove; cartilaginous ridges of mantle linear, longer than the funnel cartilage. Gladius as in *Loligo*, with long, free rhachis half as long as the gladius and with a wide vane which is rounded at the end. Rows of suckers on the arms partly increased, suckers very small; tentacle clubs with numerous rows of very small suckers."

I accept this definition of the family because the Bathyteuthidae are well characterized also by characters of the inner anatomy, as will be shown in the description of *Benthoteuthis*. However, nothing is known about the anatomy of *Ctenopteryx*, a genus recorded so far only from the Mediterranean, and it is therefore impossible to know whether the aberrant conditions in *Bathyteuthis* are also present in the inner organization of *Ctenopteryx*.

The main distinctive characters of the two genera are as follows:

Fins long, extending in adult specimens from the posterior end of the body to the anterior margin of the mantle. The transverse fin muscles are well developed and project like a comb. Luminous organs not known. *Ctenopteryx*

Fins short, about 1/4 of mantle length, with delicate muscular bridges of normal form. Eyes markedly protruding, with externally recognizable fovea. A luminous organ on the basal outer side of each of the 6 dorsal arms. *Benthoteuthis*

Benthoteuthis VERRILL

Benthoteuthis megalops VERRILL
(Plates XXIV, XXV, XXVI, XXVII)

Benthoteuthis megalops VERRILL, April 1885, *Third Catal.*, p. 401.
Bathyteuthis abyssicola HOYLE, May 1885, *Narr. Chall. Exp.*, Vol. I, p. 272, Figure 108.
Bathyteuthis abyssicola HOYLE, *Prelim. Rep. II*, p. 308, Figure 2.
186 *Bathyteuthis abyssicola* HOYLE, 1886, *Rep. Chall. Exp. Zool.*, Vol. XVI, p. 168, Plate XXIX, Figures 1–7.
Bathyteuthis abyssicola PFEFFER, 1900, *Syn. Oeg. Ceph.*, p. 173.
Bathyteuthis abyssicola HOYLE, 1904, *Rep. Ceph. Albatross*, p. 33, Plate I, Figure 2.

Localities: Station 115: Origin of Benguela Current, 36°23′S, 17°38′E. Vertical net to 2,500 m—1 specimen.

Station 207: Indian North Equatorial Current, 5°23′N, 94°48′E. Vertical net to 800 m—1 specimen.

Station 217: Indian North Equatorial Current, 4°56′N, 78°15′E. Vertical net to 2,000 m—2 specimens.

Station 221: Indian Countercurrent, 4°5′S, 73°24′E. Vertical net to 2,000 m—1 specimen.

This interesting species was described at about the same time by two authors under different names. However, the priority of *Benthoteuthis megalops* Verrill over *Bathyteuthis abyssicola* Hoyle is easily decided. Sheet 50 of the *Trans. Conn. Acad.*, Vol. VI, which contains Verrill's description, bears the note "April 1885" (p. 399), while Hoyle in the *Rep. Chall. Exped.* (1886, p. 167) writes that the first volume of the general description of the voyage (*Narrat. Chall. Exped.*, Vol. I.) appeared in "May 1885". This gives Verrill priority and *Benthoteuthis megalops* Verrill thus has priority.

B. megalops was at first known from a single specimen, caught by the *Challenger* Expedition in the subantarctic sea between the Marion and Crozet islands in 1873. Hoyle considers this form as the most remarkable of the Cephalopoda caught by the *Challenger*. This species is indeed of particular interest because of its adaptations to life in deep water.

B. megalops is at present known from all oceans. The United States Fishery Commission found 2 specimens in 1893 near the east coast of the United States; they were described by Verrill in 1885. A. Agassiz, on board the *Albatross*, obtained two specimens in the Gulf of Panama in 1891. The German Deep-Sea Expedition collected 5 specimens which are smaller than the specimens described before and some of them are juvenile. The specimens collected by the *Valdivia* were caught in the Agulhas Current south of Cape Town, near the north coast of Sumatra, south of Ceylon and of the Chagos Archipelago.

The inner anatomy and also a number of important systematic characters were not described in the earlier descriptions and I therefore give a detailed description of the external characters.

The **body** of the young specimens is spindle-shaped, especially if the short, thick arms are held
187 together. The large development of the eyes of older specimens causes a marked enlargement of the head. The tissues are gelatinous. This applies particularly to the cutis, which shows a honeycomb structure. The longitudinal muscles are situated close together, while the radial fibrous systems in the arms and mantle are separated by gelatinous tissue.

The **mantle** is long, goblet-shaped, with slightly rounded posterior end. The dorsal and ventral corners are weakly developed in the largest specimen but project more distinctly in the younger ones. The **fins** are small and widely separated. They slightly widen before their dorsal bases; they are rounded or slightly oval in the younger specimens but are not as distinctly square in the oldest specimen as reported by Verrill. The fins project only slightly beyond the tip of the mantle.

The **funnel** is of medium size. It ends anteriorly to the level of the lower third of the eye, while its ventral posterior margin forms a deep semicircular indentation. The funnel groove is shallow; the adductors are hardly visible on the outside. There is a well-developed, crescent-shaped funnel valve. The funnel organ (Plate XXV, Figure 6), which has not been described before, consists of a more or less heart-shaped mid-dorsal part with broad wings. It is 3.5 mm wide and the paired oval ventral parts are 2 mm long. All parts have a slightly rugose surface.

The **funnel cartilages** are relatively long (3.7 mm in the largest specimen). They are narrower anteriorly and have a simple groove which widens posteriorly (Plate XXVI, Figure 1). The opposite cartilage on the mantle is 4 mm long and is widened slightly posteriorly.

The **neck cartilage** (Plate XXV, Figure 7) is lanceolate, slightly wider anteriorly than posteriorly, and bears a simple median ridge. The opposite cartilage on the mantle is slightly shorter and narrower, with a median groove.

The **head** is wider than the mantle because of the large, protruding eyes. It tapers strongly toward the arms and has gelatinous cheeks which protrude slightly on each side of the funnel.

The **olfactory tubercle** has not been described before. It is small and is situated on a short, strongly pigmented lamella at the level of the lower margin of the eye.

The eye

(Plate XXVII, Figures 1–7)

The eye of *Benthoteuthis* will be described in detail because it shows marked adaptations to life in deep water. It contains structures which do not occur in other Cephalopoda and are almost unique
188 among molluscs. The eyes form an angle of almost 45 degrees with the longitudinal axis of the body; the lens is directed obliquely anteriorly and upward; the lid margin is circular and there is no distinct sinus. The back of the eye (Figure 5) is directed downward and posteriorly and bears a characteristic fovea. In younger specimens the back of the eye shines gray-bluely through the surface of the body, so that the fovea is clearly visible (Plate XXIV, Figure 8). In a small specimen of 12 mm mantle length, the eyeball is 3.5 mm long and 2.5 mm wide; it is 6.2 mm long and 4.4 mm wide in a specimen with a mantle length of 18 mm. Preparation of the eyeball shows that it is distinctly bilaterally symmetrical (Plate XXVII, Figures 1, 2), in contrast to the radial structure of the eyes of most other Cephalopoda. It is slightly laterally compressed; its dorsal surface, which faces obliquely upward, is less convex than the ventral surface. The ventral surface of the eyeball projects slightly behind the optic ganglion. The rust-red part of the iris is dorsally wider than on the ventral surface; the bilateral form of the eyeball is further accentuated by a line on the eyeball which is convex ventrally (this is the margin of the retina). The corpus epitheliale (ciliary body) is steeply raised and is slightly wider ventrally than on the dorsal side. The divided spherical lens projects markedly and is 2 mm wide in the largest eye.

Median sections of the eye show a very peculiar picture (Figure 3). The large, spherical lens is displaced slightly toward the dorsal side and is surrounded by a thick corpus epitheliale (*c. epith.*), which is raised steeply on the ventral side of the eyeball. The iris (*ir.*) originates dorsally from the posterior margin of the corpus epitheliale but extends gradually ventrally to its anterior margin. The displacement of the lens has caused the pigmented epithelium (*ep. pg.*) on the ventral surface to become much longer; it occupies the broad space between the retina and the corpus epitheliale. The retina extends dorsally to the posterior margin of the corpus epitheliale (*ret. dors.*) but ends ventrally far from it (*ret. ventr.*). If a line is drawn between the dorsal and ventral margin of the retina, one obtains a more or less hemispherical cup of the retina, the ideal main axis of which passes through the center of the optic ganglion. On the other hand, a line connecting the center of the optic ganglion with the center of the spherical lens forms a sharp angle with the main axis which measures fairly exactly the dorsal displacement of the lens.

The sclera forms a relatively thin hyaline lamella of connective tissue with large oval nuclei (Figure 6, *scl.*). On the thickened part of the retina and especially around the fovea, the sclera passes into a thin cartilaginous layer on the posterior surface of the eyeball (Figure 4, *cart.*). A slightly thicker cartilaginous lamella forms a dorsal semicircle close behind the corpus epitheliale (Figure 3, *cart.*).

The eyeball is covered on the outside by a muscular lamella of circular fibers (Figure 4, *mu.*)

189 which extends from the dorsal cartilage and covers it with especially thick fibers to near the optic ganglion; here the lamella shows a short interval, beginning again with delicate fibers on the posterior cartilage, and then thickening outside the area of the retina.

The iris forms a direct continuation of this circular muscular layer. It passes ventrally into the muscular lamella, and there is only a short interval between the cartilage and the base of the iris. On the dorsal side of the iris, there is a cartilaginous rod (*cart. ir.*) which is covered by circular fibers that form a strong sphincter on the margin of the iris. There are also smaller radial fibers, which extend outward.

The ciliary muscle is not connected with the muscular lamella which covers the bulbus. It is an independent structure which forms a sphincter between the two epithelial lamellae at the base of the epithelial body. The ciliary muscle is slightly more strongly developed on the ventral surface than dorsally. It forms on the dorsal side not only circular fibers but also radial fibers which are inserted in the dorsal cartilaginous rod and are also present on the ventral side.

Between the sclera and the pad of visual cells is a connective tissue which consists of star-shaped, branched cells (Figure 4, *bg.*). It contains numerous capillaries (*cap.*) which, as Hesse pointed out, branch also between the visual cells and reach to the cells of the limitans. The isolated rounded nuclei in this area belong to the walls of the capillaries.

The most important character of the eye concerns the ventral surface of the **retina**. As shown in the drawing, the rods become gradually longer the further distant they are ventrally from the optic ganglion and finally, in a very sharply defined pit (which is also visible from the outside of the intact eye), reach an extreme length. The rods become again short beyond the pit and finally disappear far from the epithelial body.

The unusual development of an area of maximal visual acuity in the form of a relatively wide and deep fovea which is invaginated like a funnel on the ventral side of the bulbus is certainly the most important character of the eye of *Benthoteuthis*. This structure deserves a more detailed description (Figure 4) because it is not known in other Cephalopoda.

Examination shows that the central rods (*bac.*) of the fovea are 0.4–0.5 mm long. These are the longest retinal rods known in the entire animal kingdom. They are narrower and therefore more densely arranged than in other parts of the retina. The formation of an area of maximal visual acuity characterized by an increased number of units of perception is best attained by an enlargement of the surface of the retina by the formation of a depression. The denser arrangement of the rods causes a thickening of the retina around the depression. The nuclei of the visual cells (*nu. sens.*) are here more densely arranged
190 and form numerous layers. This does not indicate that the retina consists of several layers at this point. There is only a single layer (as shown by Grenacher) of densely arranged cells with nuclei situated at different levels to make room for each other. As the visual cells are arranged radially to the depression and the rods are parallel to each other, the rods form an angle with the longitudinal axis of the visual cells.

The thickened part of the retina differs distinctly from the marginal part, which is shown in Figure 6. The rods (*bac.*) are here short and thick, while the nuclei of the visual cells (*nu. sens.*) form one row, and they show a gradual transition to an arrangement in 2 or several rows only near the fovea. The rods are only 0.06 mm long at the margin (i.e. one eighth of the length of the rods in the fovea) and nearly 0.01 mm thick.

I counted the number of rods in a sq. mm of surface of the fovea in sections of 3 eyes (my only successful section was that of the large eye, because the correct direction of sectioning was not known to me at first). Cross sections of the fovea would have been most suitable, but I had only a cross sec-

tion of the margin of the retina, where the rods form a very loose network. The rods were therefore counted in longitudinal sections. The counts showed that there were 5 rods per 0.01 mm in the center of the fovea. This corresponds to 250,000 rods per sq. mm in the central part of the fovea. According to the counts of HESSE and HESS (1905, p. 436), there are only about 105,000 rods per sq. mm in the strips of the retina of *Sepia*.

The nuclei of the retina measure 0.006–0.007 mm on the average; they are uniformly granulated, some of them rounded, others oval. The rounded nuclei occupy mainly the periphery, the oval nuclei are more numerous in the center. The nuclei form several layers; near the fovea there are 3 or 4 such layers in the center of the fovea and 9–10 laterally. This is due to the thickness of the retina which is greatest around the fovea.

It is difficult to decide whether the **pigment of the retina** is present only in cells of the limitans or also in the adjacent parts of the visual cells. At any rate, the nuclei of the cells of the limitans (Figures 4, 6, *nu.lim.*) are densely arranged outside the pigment layer. The layer of rods contains no pigment, except an occasional row of pigment granules at the base of the rods; however, pigment is completely absent in the vitreous part near the distinctly differentiated hyaloidea. In the part of the eye without retina, there is a layer of polyhedral, brown, flattened epithelial cells which continues also on the inner surface of the epithelial body.

191 The lens-shaped optic ganglion (Figures 3, 5, *g.opt.*) is 2.5 mm wide. It is situated not exactly symmetrical to the median plane of the eyeball, but is displaced slightly inward. Otherwise it shows the conditions that have already been described for other Cephalopoda. Around the optic ganglion a ring-shaped layer of cells (*c.alb.*) is situated which is slightly thicker on the ventral side than dorsally and apparently represents an indistinct white body. The main fascicle of fibers extending from the optic ganglion toward the retina is directed toward the fovea, where it ends in the thicker half of the ring of the white body.

Finally, I would like to describe a structure which has not been observed in the eyes of any other Cephalopoda. Longitudinal sections of the eye show a number of chambered formations situated inside the cranial cartilage between the optic ganglion and the fovea and forming a row which is curved like a horseshoe near the fovea (Figures 3, 5, *glom.*). The walls of the chambers (Figure 7) consist of a layer of cells, probably of connective tissue, which thickens slightly inward. These walls contain a coil of fine vessels that strikingly resemble the glomeruli of the Malpighian bodies of the kidney. This is a whorl of ascending branches which divide into extremely fine tubules. These are probably capillaries, but I was unable to find larger afferent vessels. Also interesting is the extreme rarity of nuclei in the area of the coil although nuclei are usually not rare in vessels. The glomeruli are apparently numerous, since thin sections sometimes show 10 of them close together. The function of these structures is not known.

Little is known on the **physiological function** of this peculiar eye.

The accommodation (ciliary) muscle of the eye of Cephalopoda was discoverd by LANGER (1850), who assumed that accommodation is effected by an increase of the distance between lens and retina, i.e. that an active change to the position of near vision takes place as the eye is in the state of far vision at rest. Experimental studies of this problem were begun much later. According to BEER (1897), the eyes of Cephalopoda are more or less shortsighted at rest and are actively adjusted to far vision by negative accommodation, in which the lens is approximated to the retina.

In his outstanding study on the accommodation of the eyes of Cephalopoda, HESS (1909) contra-

dicted Beer and proved that the eyes of Cephalopoda are not shortsighted in the resting state and that there is no negative accommodation. The eye of Cephalopoda is thus farsighted at rest (emmetropic or moderately hypermetropic) and there is positive accommodation by increase of the distance between
192 lens and retina. Contraction of the ciliary muscle causes a marked increase of the pressure in the eye, this increase being mainly responsible for accommodation. The increase of pressure causes the anterior part of the eye with the lens to be pressed forward and its distance from the perceptive layer of the retina to increase. Accommodation in the Cephalopoda is thus exactly the opposite of that known in fishes: the eye of fishes is myopic at rest and is accommodated negatively (by approximation of the lens to the retina), while the eye of Cephalopoda is emmetropic or slightly hypermetropic at rest and shows positive accommodation (in which the lens moves away from the retina).

In *Benthoteuthis*, however, the resting condition of the eye is one of marked myopia because of the great distance between the lens and the retina. This is certainly an adaptation to life in the dark depths. Objects situated outside the zone illuminated by the luminous organs are probably not seen, while those within the illuminated zone near the eye are perceived with an acuity which cannot be determined at present.

The main axis of the eye is directed obliquely upward (Plate XXIV, Figures 1, 8). In the best-preserved specimen, the eyes of which are intact (preservation usually results in protrusion of the eye through the lid margin), neither lens nor pupil is visible from the ventral side (Figure 7). It is probably in connection with this unusual position of the eye that the luminous organs are situated on the dorsal side of the body, in contrast to the usual condition. They are situated on the base of the 1st, 2nd and 3rd arms but are absent on the ventral arms.

The ciliary muscle is weakly developed but it probably takes part in the accommodation. Its circular fibers probably move the lens away from the fundus, assisted by the layer of muscular fibers situated outside the eyeball.

Dark adaptation is demonstrated by the distribution of the pigment. As shown by Rawitz (1891) and in greater detail by Hess (1905), exposure of the retina to light and darkness causes extensive movement of the pigment in the eyes of surface forms. In light, pigment granules move into the rods, surround the axial threads (described by Grenacher) and concentrate so densely around their terminal knob that sections sometimes show a uniform stripe of pigment. In the dark, the pigment is retracted from the layer of rods. Hess (1905, p. 436) showed that pelagic and littoral surface Cephalopoda have a narrow central zone of the retina in which the rods are much longer and narrower than in other
193 parts of the retina. In this so-called "stripe" the pigment advances more slowly in light than it does in the other parts of the retina, but returns more rapidly in the dark. After a brief exposure to light or dark, this stripe can therefore be clearly distinguished from the other part of the retina in a freshly opened eye. The speed of the advance or retreat of pigment varies in the different species. In *Sepia* that had been kept for 4 hours in the dark, the pigment had retreated to the base in the whole retina; the pigment of another specimen kept in semidarkness formed dense (vitral) knobs on the inside after 3 hours, also in the stripe. Other forms showed such movement of pigment after longer periods of light or dark.

All the retinae of the pelagic deep-sea Cephalopoda examined, particularly those of *Benthoteuthis*, show a dark position of the pigment. This condition agrees so well with the pelagic nature of deep-sea forms that it is doubtful whether pigment movement takes place at all.

This description of the eye of *Benthoteuthis*, and a previous communication of mine (1903), induced Hess (1905, p. 435) to distinguish 3 stages of development of the retina. In the first stage, the retina is uniformly thick throughout and contains uniformly dense rods (*Loligo*, *Todaropsis*). Other

retinae have a zone of optimal vision in which the rods are much longer and thinner than in the surrounding area (*Rossia*, *Scaeurgus*, *Eledone*, etc.). *Benthoteuthis* forms a third group whose area of optimal vision resembles a fovea having very long and thin rods.

Arm apparatus
(Plate XXV)

The arms are thick, short, three-edged and of about the same size; the 4th arms of the largest specimen are the longest, 6 mm, the 2nd arms are nearly as long, the 3rd arms are slightly shorter than the 2nd, and the 1st arms are slightly shorter than the 3rd. The arm formula is thus 4, 2, 3, 1, as reported by VERRILL (1885, p. 403); but this does not agree with the arm formula 1, 2, 3, 4 given by HOYLE (1886, p. 169).

All except the ventral arms have small swimming membranes. They are connected at the base by outer membranes which extend broadly from the 1st to the 2nd, from the 2nd to the 3rd and from the 3rd to the 4th arms but are absent between the 4th arms (Figure 3).

The protective membranes are well developed throughout and have strong muscular supports. The dorsal protective membranes are less developed than the ventral ones; those of the 4th arms are the
194 smallest. The delicate membrane which connects the muscular supports is absent in the large specimen, so that the supports appear like cirri. On the other hand, this membrane was well developed in younger specimens.

The suckers bear 5 to 6 denticles on the dorsal margins. They are arranged in two rows only in the proximal third or quarter of the arm; they form 3 or 4 rows on the other parts of the arm. The biserial pattern is present to the middle of the ventral arms and almost to the tip of all arms in younger specimens.

The ventral arms thus differ from the other arms in the larger, dorsally displaced swimming membranes and the weakly developed protective membranes; the sucker-bearing area is narrower and the biserial arrangement of suckers extends to the middle of the arms.

The **tentacles** have a rounded stalk with flattened inner side. The club is not thickened and has no swimming membranes but a narrow keel (swimming membrane) which is slightly displaced dorsally (Figure 4). The small, densely arranged suckers permit no clear distinction of a carpal and a hand part; they begin proximally in a single row which gradually passes into 3, 4 and in the middle into 8 to 10 longitudinal rows. The juvenile club (Figure 5) shows an indication of this condition but with fewer suckers in a transverse row.

The base of the tentacle is visible through the skin to the middle of the eye or to the funnel adductors in younger specimens (Plate XXIV, Figure 7). The base of the tentacles is spindle-shaped, as in *Pterygioteuthis*, and then becomes narrower and forms a lyre-shaped curve anteriorly.

The **buccal membrane** has 7 points; it is smooth on the outside but distinctly wrinkled on the inside. HOYLE (1886, p. 168) observed the presence of two small suckers on the inner side of each of the 7 points—a unique character in Oegopsida. I found two such suckers on each point in the larger specimens (Plate XXV, Figure 3); the medium-sized specimens had only one sucker at each point, and the smallest had still no sucker at all (Figure 2).

The **attachment of the arms** is of the same type as in the Enoploteuthidae (p. 15): the 1st and 2nd arms are attached dorsally, the 3rd arms are attached ventrally, and the 4th arms, again, dorsally (Figure 3).

Coloration

The **coloration** is of a vivid purple. It is caused by two layers of chromatophores and by branched, star-shaped, pink connective-tissue cells which belong to the cutis. The pigmentation is most intensive on the outer side of the arms, on the head and around the eyes; that of the ventral surface and the outer and inner sides of the fins is slightly weaker; the tentacle stalks are colorless.

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Luminous organs

(Plate XXVII, Figure 8)

Earlier authors did not notice the luminous organs of *Benthoteuthis*. There is an oblong, slightly protruding organ which is apparently a luminous organ on the outer side of the base of the 1st, 2nd and 3rd arms (Chun, 1903, p. 69). These six organs are about 0.5 mm wide in younger specimens, 0.7 mm in larger specimens. They are surrounded by dark pigment and there is usually a sharply differentiated whitish, slit-shaped mass in the middle. However, they were completely covered by pigment in many cases, which suggests that the outer layer of pigment is movable. These organs are situated close to the longitudinal muscular layer of the arms (*mu.l.*); they are covered on the outside by the gelatinous cutis, as is distinctly revealed e.g. in a young specimen preserved in formol. I made sections of a few organs of a young specimens fixed in chrome-osmic acid; one of them is shown in Figure 8. The organ receives proximally a thick nerve (*n.*) the fibers of which extend into a peculiar tissue, probably the luminous body (*phot.*), which in general shows a fibrous structure with scattered nuclei. This fibrous structure is most distinct distally and least distinct in the proximal part. The latter contains numerous oval or rounded nuclei, 0.005–0.1 mm wide and finely granulated, but there are no distinct cell boundaries around them. The organ contains numerous capillaries (*cap.*) the cross sections or looped branches of which are more distinct in the distal half.

Reflectors or lens-shaped thickenings are absent, but the organs have a dark pigment sheath (*pg.*) in the proximal part which continues for some distance beyond the entering nerve. The pigment becomes sparser distally, but isolated chromatophores (*chrom.*) are present on the outer surface. Cross sections of these organs gave no new information. The whole structure suggests that if this nucleated central tissue is indeed a luminous body, the emitted light is directed distally and perhaps receives a certain color from chromatophores which change their position.

The organs of *Benthoteuthis* are situated mainly on the dorsal side, while those of all other Oegopsida are situated mainly on the ventral side. This is obviously correlated with the dorsal position of the eyes. The beam of light emitted from the organs is directed anteriorly, preventing direct illumination of the eye.

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Mantle complex and inner organs

(Plate XXV, Figure 1; Plate XXVI)

Although my largest specimen of *Benthoteuthis* is smaller than those described previously, examination of the soft parts, taking care not to damage the object, seemed promising. This was confirmed in some points, especially with regard to the intestinal tract and vascular system.

Opening of the mantle cavity (Plate XXV, Figure 1) shows a delicate septum in its posterior quar-

ter the anterior margin of which is bordered by the pallial artery. Anteriorly are situated the funnel with its semicircularly indented ventral margin, the funnel cartilage, and the mantle cartilage. Also visible are the two large musculi depressores infundibuli which originate broadly on the dorsal wall of the funnel and taper rapidly posteriorly into a thin muscular strip near the base of the gills. Close to their inner margin pass the musculi recti abdominis of the visceral sac, which extend to the venous sacs. Situated slightly deeper are the two lateral retractors of the head (Plate XXVI, Figure 1, *mu. retr. cap. lat.*) in the form of broad lamellae which surround the anterior half of the liver like a dish and diverge posteriorly, extending in a point to the depressors.

Anus, branchial heart and gills are visible and so are the small nidamental glands which prove that the specimen is a young female. The heart and venous appendages are visible through the abdominal wall and so is part of the caecum and the grapelike ovary. The honeycomb-shaped pancreatic appendages are also indistinctly visible in front of the base of the gills, while the greater part of the liver is covered by the muscular envelope.

Intestinal tract
(Plate XXVI)

I thoroughly examined only the posterior part of the intestinal tract; it shows a number of characteristic structural conditions.

The **esophagus** (Figures 1, 3, *oes.*) extends dorsally on the median part of the liver, which forms a shallow groove which contains also the cephalic aorta, (*a. ceph.*), situated on the right side of the esophagus. The esophagus bears longitudinal folds and opens at the posterior margin of the liver into the stomach, which consists of a thin-walled anterior part (*st.'*) and a sac-shaped posterior part (*st.*). The anterior part passes broadly into the caecum (Figure 3, *o. st.*) which is situated ventrally and slightly
197 left of the stomach. The caecum is kidney-shaped and large, but shorter than the stomach; its entire ventral side is covered with folds which extend spirally from the opening of the pancreatic ducts (*st. coec.*). The mid-intestine is wide and almost completely covered by the pancreatic appendages. It passes almost imperceptibly into the rectum (*rect.*), which opens between two small, spatulate anal appendages (*an.*). The terminal part of the intestinal tract is held in position by a ligament (Figure 2, *lig. an.*) which extends from the median surface of the liver to the rectum.

The **liver** (*hep.*) has a characteristic form. In most Oegopsida the liver is spindle-shaped and situated obliquely, sometimes even transversely to the longitudinal axis of the body. The liver of *Benthoteuthis* is situated rather exactly in the longitudinal axis of the body. It is large and sac-shaped and extends unusually far anteriorly, to the posterior salivary gland (Figures 2, 3, *saliv. post.*) and thus to the visceral ganglion. The liver narrows here slightly and adheres to the posterior side of the cranial capsule, so that it apparently ends in two blunt processes (Figure 3). The anterior half of the liver (*hep.'*) differs from the norm in that if forms a thin-walled sac filled with liquid. The liver has a compact structure only at the posterior end and on the ventral side along the rectum, this structure having a honeycomb pattern on the outside. There are two large openings (Figure 2, *d. hep.*) on the lateral posterior margin which pass into the pancreas.

The **pancreas** (*pancr.*) is also of unusual form. It consists of two large, thin-walled complexes of glands which are convex anteriorly. The surface shows large, polyhedral cells which project spherically. The two honeycombed pancreatic ducts open ventrally in the caecum at the point at which the folds originate.

The posterior salivary gland (Figures 2, 3, *saliv. post.*), is ovoid in form and is situated between the esophagus and the anterior end of the liver.

I could distinguish only the efferent duct of the inc sac (*atr.*) which opens into the rectum behind the anus.

The important characters of the intestinal tract are thus the kidney-shaped caecum, which is shorter than the stomach, and especially the peculiar form of the glandular appendages. Unfortunately, these structures lack any clue that would be helpful in establishing a familial relationship. A structure resembling the liver of *Benthoteuthis* has not been found in other Cephalopoda, nor has a pancreas with a large lumen and honeycombed walls its like elsewhere; only the pancreatic gland of *Bathothauma*, one of the most aberrant genera of the Cranchiidae, comes to mind, but then that gland is much more compact.

198 **Vascular System** (Plate XXVI, Figures 4, 5). The vena cava (*v. c.*) becomes visible directly behind the heart-shaped indentation of the median funnel organ and then passes on the right side of the rectum at the level of the posterior margin of the pancreas and ends in two small venous sacs (*s. ven. hep.*). Each of these sacs receives a large vein (*v. hep. pancr.*) from the pancreas. The vein branches here into two crescent-shaped arms (*s. ven.*) covered with venous appendages which open in the branchial hearts. They also receive the abdominal veins (*v. abd.*) and the pallial veins (*v. pall.*). The branchial hearts (*c. branch.*) are oval, and dorsal examination (Figure 5) shows the small appendage of the branchial heart (*app. c.*) near the entrance of the venous branches. The branchial arteries (*a. branch.*) extend from the branchial hearts to the loose, relatively short gills (which are 4 mm long in the larger specimen). Blood returns to the heart through the branchial veins (*v. branch.*), which are not markedly dilated at their opening. The heart (*c.*) is spindle-shaped and almost transverse; it is situated slightly to the right. At its right corner originates the cephalic aorta (*ao.*), at its left corner the posterior aorta (*a. post.*).

The **renal sac** is thin-walled; it opens in two slightly raised, chimneylike pores of excretion (Figures 4, 5, *ur.*) at the level of the anterior margin of the pancreatic appendages, close to the vena cava. Exposure of the abdominal wall also shows the long, thin ducts of the body cavity (Figure 5, *d. coel.*) with the inner openings of the renal sacs.

The **genitalia** of the largest specimen are typical for a young female. The ovary (*ov.*), containing developing eggs, resembles a cluster of grapes. It is situated on the right side of the stomach and is connected with the posterior end of the body by a cord of connective tissue, the ligamentum gastrogenitale (*lig. g. g.*). Examination from the ventral side shows the small nidamental glands (Figures 4, 5, *nid.*), situated on each side of the anterior venous sacs. The small oviducts (*ovid.*) are situated dorsal to the branchial hearts and are in a very early stage of development; they are most distinct if the abdominal wall is examined from the dorsal side (Figure 5). The developing oviduct glands cause a slight swelling of the anterior part; the posterior part forms a simple loop.

The above description shows that *Benthoteuthis* occupies a rather isolated position among the Oegopsida. The relationships of this genus are still not clear. The attachment of the arms resembles that of the Enoploteuthidae, Histioteuthidae and Ommatostrephidae. On the other hand, the form of the intestinal tract and especially the form and position of liver and pancreas are so aberrant that closer relationships cannot be established. The numerous paired suckers at the end of the arms and
199 the presence of suckers on the points of the buccal funnel are characters not known in other families of Oegopsida. *Benthoteuthis* shows some similarities with *Ctenopteryx* in the form of the club, the

funnel cartilage and the gladius, but we agree with HOYLE that it is doubtful whether these two genera belong to the same family. PFEFFER places the two genera in the family Bathyteuthidae and this is provisionally accepted.

Measurements of the Largest Specimen (Station 221)

Dorsal length of mantle	18	mm
Width of mantle	8	mm
Length of fin	4	mm
Width of fin	3	mm
Width of head	10	mm
Length of 1st arm	5	mm
Length of 2nd arm	6	mm
Length of 3rd arm	5.5	mm
Length of 4th arm	6	mm
Length of tentacles	18	mm

Ctenopteryx APPELLÖF

Ctenopteryx siculus RÜPPEL and VÉRANY
(Plate XXVII, Figures 9, 10, 11)

Sepioteuthis sicula RÜPPELL; VÉRANY, 1851, p. 75, Plate 2.
Chtenopteryx fimbriatus APPELLÖF, 1889, p. 4, Figures 1–6.
Chtenopteryx cyprinoides JOUBIN, 1894, p. 4, Figure.
Calliteuthis neuroptera JATTA, 1896, p. 118, Plate XXXI, Figures 1–10.
Ctenopteryx siculus PFEFFER, 1900, p. 172.
Ctenopteryx cyprinoides JOUBIN, 1900, p. 47, Plate XIV, Figures 3–5.
Ctenopteryx neuroptera JATTA, 1904, p. 201.
Ctenopteryx fimbriatus et *neuroptera* ASHWORTH and HOYLE, 1906, pp. 2, 5, 7.
Ctenopteryx fimbriatus et *neuroptera* HOYLE, 1909, p. 271.

Locality: Station 86, outer border of the Benguela Current, 28°28′S, 6°13′E. Vertical net to 2,000 m—One juvenile specimen.

ASHWORTH and HOYLE (*Mem. Manchester Lit. Philos. Soc.*, Vol. 50, 1906) have recently published a critical revision of the species of *Ctenopteryx* described. I agree with them only in the point that *Ctenopteryx fimbriatus* APPELLÖF is identical with *Ctenopteryx cyprinoides* JOUBIN and *Calliteuthis neuroptera* JATTA. However, I think that *Sepioteuthis sicula*, discovered by RÜPPELL and described by VÉRANY (1851, p. 75, Plate 27), also belongs to this species. ASHWORTH and HOYLE consider *S. sicula* as a doubtful form of undefined systematic position. Sheet 5 of RÜPPELL's drawings, in the Sencken-
200 berg Library, Frankfurt a.M., shows a drawing of *Ctenopteryx* ("Messina, 10 March 1844") which is so exact that its identity cannot be doubted. In particular, the characteristic muscles of the fins, which extend to the anterior margin of the mantle, are shown correctly and far more clearly than in the later figure of VÉRANY. It is therefore my opinion that this species has to be named *Ctenopteryx siculus* RÜPPELL.

This form was known only from the Mediterranean but our expedition collected it also in the

southern Atlantic (Station 86). The specimen is a juvenile stage (Plate XXVII, Figures 9–11) of 7 mm dorsal mantle length, i.e. still smaller than Appellöf's specimen, which has a mantle length of 10 mm.

The mantle is sac-shaped, rounded posteriorly and with an almost straight margin. The gladius with its broad, shovel-like posterior end which bears laterally the two delicate fins is visible in the dorsal midline. The fins are 3 mm long; they are contiguous only at the posterior end of the body, while they diverge anteriorly at an angle of 60°. The pointed anterior end of the fin projects slightly beyond its dorsal base (Figure 11). The characteristic comblike pattern of the transverse muscular bridges, of which there are about 18 on each fin, proves that this is a larva of *Ctenopteryx*. The delicate connecting membrane is torn, especially at the free margin, and some muscular bridges project like cirri. Since the small fins occupy barely one third of the mantle length, it is prima facie doubtful whether the specimen belongs to *Ct. cyprinoides* in which the fins extend to the anterior margin of the mantle. However, we know from the postembryonic development of all Oegopsida with large fins, that these are at first very small and grow anteriorly only secondarily. We can therefore consider the larva without doubt as belonging to *Ct. cyprinoides*, the more so as a later lengthening along the mantle is indicated by the divergence of the dorsal base of the fins.

The head is not wider than the mantle and is slightly retracted into it. The eyes are of medium size, with a weakly indicated sinus. The funnel with its wide opening is situated in a shallow groove.

The arms are short, with angular edges, and of about equal length. However, only the 3rd and 4th arms are exactly equal: the 2nd and 1st arms are slightly shorter; the arm formula is therefore 4, 3, 2, 1. Swimming membranes are well developed, especially on the 3rd and 2nd arms; those on the 4th arms are displaced slightly toward the dorsal side. The arms bear small suckers, which are arranged in two rows throughout on the ventral arms; the other arms show an irregular arrangement in 2 or 4 rows at the tip.

The tentacles are still very short, with a rounded stalk, and the club is only slightly widened into a spoon. The club closely resembles that of the older stage illustrated by Appellöf. There is no difference between the carpal and hand part; the small suckers are arranged proximally in 3, 4 and 5 rows, but they increase in number and size, forming up to 9 rows in the middle of the club. Distally
201 the suckers become rapidly smaller again, but the number of rows does not decrease distinctly. There is no visible swimming membrane and no protective membrane.

This brief description shows that important systematic characters, such as the comblike form of the fins, the increased number of suckers at the end of the arms and the large number of rows of suckers on the tentacles, develop early and permit a definite determination of the larvae as those of *Ctenopteryx siculus*. The occurrence of this species is thus not restricted to the Mediterranean. In addition to our record from the southern Atlantic, the *Gauss* expedition later collected a slightly younger larva of this species in the same area, i.e. northeast of Tristan da Cunha.

6. Family **Ommatostrephidae** STEENSTR.

Ommastrephini STEENSTRUP, **1861**

Rhynchoteuthis CHUN, 1903

A juvenile form of Ommatostrephidae

Poulpe (jeune âge). EYDOUX and SOULEYET, Voy. "Bonite". *Zool.*, Part II, 1852: *Mollusques*, p. 17, Plate 1, Figures 15–21.
Decapodo incertae sedis. JATTA, *Boll. Soc. Naturalisti Napoli*, anno 3⁰, fasc. 1⁰, 1889, p. 67.
Rhynchoteuthis CHUN, 1903, *Zool Anz.*, p. 716.
Rhynchoteuthis chuni HOYLE, 1904, *Rep. Ceph. "Albatross,"* p. 32, Figure G.
Rhynchoteuthis ISSEL, 1908, *Cef. "Liguria,"* pp. 215, 217, Plate IX, Figures 12–14.
Rhynchoteuthion PFEFFER, 1908, *Nord. Plankton*, IV, Ceph., p. 88.

In a brief communication (*Zool. Anz.*, Vol. XXVI, 1903, p. 716) I mentioned a number of larvae of peculiar form which belong to the developmental cycle of the Ommatostrephidae. The larvae described here apparently belong to different species but have one character in common: the tentacles are fused their whole length into a snoutlike process. By this character the larvae are easily recognized already in the earliest stages and can be arranged in a developmental series. The youngest larvae are little longer than 1 mm; the oldest larvae are 10 mm long with extended tentacles and their mantle length is 4–5 mm. In the older stages the cylindrical snout diverges at its base into two muscular pillars with a triangular opening between them. The snout tapers slightly towards the tip and forms there two triangular lips, each with 4 suckers. The two dorsal pairs of arms develop first; the 3rd arms appear later and the ventral arms last. The arms of older stages bear two rows of small suckers. The relatively slender, cylindrical body bears small, rhomboidal terminal fins.

The systematic position of these peculiar forms is determined by one important character: the
202 strongly developed funnel cartilage, which closely resembles that of the Ommatostrephidae as it has a wide, posteriorly constricted longitudinal groove which passes into a transverse groove. The form of the mantle cartilage also resembles that of the Ommatostrephidae.

These larvae are not rare; our expedition found about 35 larvae, which apparently belong to different species, in the Atlantic and Indian oceans. There are two types: some larvae are slender, with eyes of moderate size, others have a plump body and large eyes with a clearly differentiated pitlike fovea of sharpest vision.

The snoutlike tentacle apparently divides later into two halves from the divided base. HOYLE (1904) described an older larva of this type from the Pacific Ocean; the tentacles of this specimen were already separated, except at the tip.

I named these bizarre larvae *Rhynchoteuthis*, but their relationship to known genera cannot be determined at present. HOYLE drew my attention to the fact that this name had already been given by D'ORBIGNY to a fossil genus of Cephalopoda (*Moll. viv. et foss.*, 1845/55, p. 593). PFEFFER (1908, p. 88) therefore changed the name to *Rhynchoteuthion*. The name is not important, as it is intended only provisionally for juvenile forms the relationship of which to known species needs further research.

Perusal of earlier literature has convinced me that these forms are not quite unknown, although they have been interpreted in rather strange ways. Thus, Eydoux and Souleyet (Voy. "Bonite", *Zool.*, Part II, 1852, *Mollusques*, p. 17, Plate 1, Figures 15–21) described a young stage of *Rhynchoteuthis* as "Poulpe (jeune âge)?". Because of the small number of arms (the ventral arms are not yet developed), they placed it provisionally in the Octopoda. De Blainville examined the two specimens from the Pacific Ocean and considered the snout to be a remnant of the yolk sac, while Eydoux and Souleyet at least correctly maintained that this mysterious structure seems to be muscular.

I noticed later that Jatta had described a larva of this type and gave a correct interpretation of its organization in a little known journal ("Elenco de Cephalopodi della 'Vettor Pisani'", in: *Bolletino di Naturalisti in Napoli*, Anno 3^0, 1889, p. 67, No. 18) under the name "Decapodo incertae sedis". Jatta recognized that this was a larva of Decapoda, the tentacles of which are fused into a snoutlike process, but he did not realize that it belonged to the Ommatostrephidae.

The peculiar form of these larvae is best described by means of the illustrations on Plates XXVIII and XXIX, beginning with stages which can be arranged in a developmental series on the basis of their relatively slender form and their medium-sized, nonprotruding eyes.

203 The youngest larvae (Plate XXVIII, Figures 1, 2, 3 and 10) are 1.2–1.8 mm long. The mantle of the specimen shown in Figure 1 is 0.8 mm long, sac-shaped and covers the anterior part of the body to the eyes; in the other specimens the mantle does not cover the head or the funnel, which is curved downward. The tentacles of all these larvae form a snoutlike process which is fused to the base and which already bears eight apical suckers. The process is apparently very contractile, since it is short and thick if retracted but becomes slender and curved if it is extended.

In addition to these snoutlike tentacles, only the two dorsal pairs of arms are present, each with a single sucker. The larger of these very young larvae already show the "anlagen" of the 3rd arms as stumps near the bases of the 2nd arms; however, there is no trace of the 4th arms. The ovoid mantle is covered with a few large, symmetrically arranged chromatophores and some chromatophores are present also on the head. The posterior end of the body bears minute, spatulate fins.

Figures 4–7 show a group of medium-sized larvae of about 2 mm mantle length, with better developed fins. The spindle-shaped body of these specimens continues anteriorly in the snoutlike process of the tentacles that may be short and straight or long and curved downward. The process bears 4 suckers on each side at the tip at the inner margin of the lips; one of the middle suckers is larger than the lateral suckers (Plate XXIX, Figure 6).

All medium-sized larvae have well-developed 3rd arms which are nearly as long as the 1st and 2nd arms (Plate XXIX, Figure 1). The stump-shaped "anlagen" of the 4th arms are distinct in these larvae. Each of the arms bears 2–4 pairs of suckers.

The pigmentation consists of loosely arranged chromatophores in a bilateral symmetrical arrangement on the head.

The oldest stages (Figures 13–15) have a goblet-shaped mantle of 4.5–5 mm dorsal length, with a pointed posterior part which bears two rhomboidal fins and ends at the level of the tip of the mantle. The mantle corners are more distinct, and so are the outer adductors, lateral to the funnel groove, which are so characteristic for the Ommatostrephidae. Near them are the small knob-shaped olfactory tubercles (Plate XXIX, Figure 4). The neck cartilage consists of a narrow, band-shaped ridge with a median groove into which fits a ridge of the opposite cartilage (Plate XXIX, Figure 3).

The funnel cartilages are unusually large and distinct, of the type of the Ommatostrephidae (*ibid.*, Figure 4). The corresponding mantle cartilages bear a noselike longitudinal cartilage with a weakly developed transverse cartilage posteriorly.

The ventral margin of the funnel is convex anteriorly and covers the anus and the anal appendages. The latter (Plate XXIX, Figure 8) have on one side a flag-like membrane which extends to the base.

The **arm apparatus** is much further developed, but the tentacles are still fused almost to the base,
204 where the two roots diverge and form an oblong triangular opening between them. The tentacles still bear 8 suckers at the tip, as in the previous stages. All arms are developed, but the ventral arms are still much shorter than the others. Seven or 8 pairs of suckers are present on the 1st, 2nd and 3rd arms; the 4th arms bear only one to two pairs of suckers (Plate XXIX, Figure 2).

The **pigmentation** is still very weak. The dorsal chromatophores on the mantle are slightly larger but less densely arranged than those on the ventral side, which also has a darker chromatophore at the base of each fin. The bilateral arrangement of the chromatophores on the head persists. There are two median and 3 pairs of lateral chromatophores on the dorsal side of the head. The ventral side of the head bears 8 chromatophores, also in a bilateral arrangement. Each arm of the first three pairs bears a single row of 3 or 4 large chromatophores.

A second series of stages consists of larvae with very large eyes and a slightly plumper body. Canada balsam preparation of the eyes of the younger specimens shows that the pigment layer forms a funnel caused by the fovea which projects deeply posteriorly (Plate XXIX, Figure 5).

The youngest stage (Figure 8), a specimen with very large chromatophores on the ovoid mantle and very small fins, belongs to this developmental cycle because it has a distinct fovea of the above type. This stage is 1.5 mm long, including the tentacles. Only the 1st and 2nd arms are developed, and each arm bears a small sucker.

The intermediate stage shown in Figure 9 has a mantle length of 1.8 mm. The "anlagen" of the 3rd arms are already present in form of short processes.

The older larvae (Figure 11) are plump, with a sac-shaped mantle of 2.5 mm dorsal length and with two small, spatulate fins. The funnel projects beyond the mantle, and the head is very wide because of the two large, slightly protruding eyes. The tentacles are curved downward and are not divided at the base; they bear 8 suckers at the tip. All arms are present, but the ventral arms form only small stumps. The arm formula is 3, 2, 1, 4. The 2nd and 3rd arms bear 5 pairs of suckers; there are only 3 pairs of suckers on the 1st arms. The chromatophores are sparse; the dorsal side of the mantle shows only 5 chromatophores in a symmetrical arrangement, the dorsal side of the head 2 median and 3 lateral pairs of chromatophores.

Figure 12 shows the largest stage, with 4 mm dorsal mantle length. The anterior margin of the sac-shaped mantle covers the funnel and the posterior half of the eyes.

205 Opening of the mantle cavity shows the funnel cartilage typical for the Ommatostrephidae. The anal appendages differ from those of the more slender larval stages with small eyes in that they have a crescent-shaped membrane on one side only in the distal half (Plate XXIX, Figure 7). The eyes protrude markedly, while the arm apparatus is relatively less developed than in larvae of equal size of the previous series. The snoutlike tentacles are short, 1.2 mm long, with the usual 8 suckers at the tip. The arm formula is 1, 2, 3, 4, but the 1st and 2nd arms are of almost equal size. All except the stump-shaped 4th arms bear 5 pairs of distinct suckers and very small suckers at the tip.

It appears to be characteristic for the larvae of all Ommatostrephidae that their tentacles are fused into a snoutlike process which becomes divided into two separate tentacles at a later stage. This is suggested by the different form of the larvae and the fact that no young larvae of Ommatostrephidae with separate tentacles have been found. If this is correct, it would provide an excellent character for the recognition of the larvae of the Ommatostrephidae.

7. Family **Tracheloteuthidae** Pfeffer

Chiroteuthidae p.p. Verrill, 1881, p. 431.
Tracheloteuthidae Pfeffer, 1900, pp. 152, 174.
Tracheloteuthidae Hoyle, 1909, p. 271.

Body slender; posterior end pointed, with large terminal heartshaped or rhomboidal fins. Head rounded, distinctly demarcated from the narrower neck, with folds. Funnel cartilage with a simple longitudinal groove which has narrow margins and which widens slightly posteriorly; mantle cartilage in the form of a linear ridge, longer than the funnel cartilage. Gladius consisting almost entirely of the rhachis anteriorly, posteriorly with a long cone the margins of which are fused at the tip. Arms with two rows of suckers. Ventral arms attached ventrally. Tentacle stalk with numerous suckers in 2 or 4 rows in the distal part. Middle of club with numerous (up to 16) longitudinal rows of suckers. Proximal half of club with small suckers; distal half with large suckers which become gradually smaller and pass into 4 rows toward the tip. Funnel depressors in the form of broad bands and contiguous in the middle.

The juvenile forms have been described as *Verrilliola* Pfeffer **and** *Entomopsis* Rochebrune.

206 ## *Brachioteuthis* Verrill

Brachioteuthis Verrill, Nov. 1881, p. 405.
Tracheloteuthis Steenstrup, 1882, p. 294.
Verrilliola Pfeffer, 1884, p. 22.
Entomopsis Rochebrune, 1884, p. 15.
Tracheloteuthis Hoyle, 1886, p. 164.
Tracheloteuthis Weiss, 1888, p. 85.
Tracheloteuthis Lönnberg, 1896, p. 603.
Tracheloteuthis Fowler, 1897, p. 523.
Tracheloteuthis Steenstrup, 1898, p. 111.
Entomopsis Joubin, 1899, p. 72; 1900, pp. 90–92.
Tracheloteuthis Pfeffer, 1900, p. 175.
Brachioteuthis Pfeffer, 1900, p. 176.
Tracheloteuthis Hoyle, 1905, p. 93.
Tracheloteuthis Pfeffer, 1908, p. 78.
Brachioteuthis Russell, 1909, p. 449.
Brachioteuthis = *Tracheloteuthis* Hoyle, 1909, p. 271.

The genus *Trachelotheutis* Steenstrup 1882 is apparently identical with the genus *Brachioteuthis*, established by Verrill in November 1881. In his "Synopsis" Pfeffer listed *Tracheloteuthis* as a separate genus, but later expressed his doubts about its validity and mentioned this recently (*Nordisches*

Plankton, IV, *Cephalopoden*, p. 79). Hoyle (*Catalogue of Recent Cephalopoda*, 1909, p. 271) also considers *Branchioteuthis* as identical with *Tracheloteuthis*.

Pfeffer (*loc. cit.*) proved that the name *Brachioteuthis* has priority over *Tracheloteuthis* because Steenstrup's paper was published after April 1882, while that of Verrill bears the note "November 1881".

The differences between *Brachioteuthis* and *Tracheloteuthis* consist mainly in the relative size of the fins and the different coloration, but these, according to my observations, are apparently connected with the postembryonic development. Since all morphological characters are very similar, we are apparently dealing with two species of the same genus, which should be named *Brachioteuthis*.

I agree with Pfeffer that the specimens described by him as *Verrilliola* (1884) are the juvenile forms of *Tracheloteuthis*. The same applies to the forms described by Rochebrune as *Entomopsis*; the strange habitus of these forms will be described later for young stages. Hoyle (1905), in a critical study of the species placed by Steenstrup in *Tracheloteuthis*, proved that the relative size of the fins and arms varies with age and that all these forms belong to a single species, *Tr. riisei*. The following diagnosis is therefore confined to the 4 species which belong to this genus in my opinion:

207 Mantle produced posteriorly in a short point. Fin shorter than half of mantle length. Club narrow. Coloration pale; head with a few large chromatophores.

Br. riisei Steenstrup

Mantle produced posteriorly in short point. Fins half as long as mantle. Head narrower than mantle margin. Club narrow, straight. Coloration purple brown.

Br. beanii Verrill

Mantle produced posteriorly in a long, blunt point. Fins half as long as mantle. Head slightly wider than mantle margin. Club wide, its apex curved dorsally like a chamois horn. Coloration vivid purplish brown.

Br. picta Chun

Mantle produced posteriorly in a sharp point. Fins one third as long as mantle. Head wider than mantle margin. Eyes very large. Club wide. Coloration purplish brown.

Br. bowmani Russell

Verrill placed the genus *Brachioteuthis* in the family Chiroteuthidae, while Pfeffer established a new family for it. Verrill was certainly guided by certain similarities in the external morphology, mainly the rounded head and the slender neck. However, the Chiroteuthidae have no neck folds and their funnel cartilage contains a tragus and an antitragus. The new family may thus be considered valid according to present knowledge. Among the characters which prove closer relationship to the Chiroteuthidae and which were not considered by earlier authors is mainly the bandlike form of the funnel depressors (Text Figure 1, p. 5). As there are also some common characters of the inner organization, I consider the two families to be closely related.

Brachioteuthis picta Chun

(Plate XXIX, Figure 11; Plate XXX, Figures 4, 5; Plate XXXI, Figures 1–3, 5, 7, 8; Plate XXXII)

Locality: Station 67, branch of the Benguela Current, 5°6′N, 9°58′E. Vertical net to 1,500 m—One male.

The head is fleshy, brightly colored, arrow-shaped. The eyes are large and slightly protruding. The arm apparatus is moderately developed.

The mantle is long and narrow and ends in a long, spearlike point. The mantle corners project markedly, especially the dorsal corner.

The fins are half as long as the mantle, heart-shaped or nearly rhomboidal. They show a deep, heart-shaped indentation anteriorly and are fused dorsally without projecting beyond the tip of the mantle. HOYLE (1905, p. 95) noted that the fins of *Tr. riisei* become the longer the older and larger the animal, but they do not attain half of the mantle length, which contrasts with our specimen the genitalia of which show that it is a young male.

208 The **funnel** is of medium size and has a strongly curved posterior ventral margin. It is situated in a shallow funnel groove which is filled by the 4 long adductors. The median adductors are smaller and narrower than the lateral ones. The mid-dorsal part of the funnel organ resembles an arrowhead and is 3 mm long; both lateral parts are 3 mm long, too, and shaped like a hatchet.

The funnel cartilage is 4 mm long, 1,5 mm wide posteriorly, slightly narrower anteriorly. It bears a simple, deep groove that is surrounded by medium-sized margins which continue anteriorly as a short cartilaginous strip. The mantle cartilage is almost 5 mm long and forms a narrow ridge which projects beyond the anterior end of the gill (Plate XXXII, Figure 1).

The neck cartilage (Plate XXXII, Figure 5) is spatulate, with swollen margins. Two median ridges pass along a groove into which fits the ridge of the narrower opposite cartilage.

The **neck** is retracted and is delimited from the wide head by 3 swollen ridges or folds which extend obliquely posteriorly (Plate XXXII, Figure 2). The anterior fold is situated at the level of the funnel opening; the middle fold projects only slightly and bears the finger-shaped olfactory tubercle; the posterior fold is wide and low. In addition to these 3 longitudinal folds there is an indistinct transverse fold closely in front of the 3 folds.

The **head** is rounded because of the large, slightly protruding eyes. The eye is 4.5 mm long and 4 mm wide; the lens is 2 mm wide. The iris is blackish only at the margin of the lens; it has a metallic sheen, like the epithelial body. A light, glossy stripe extends from the white body to the arms on the ventral side of the eye. This stripe becomes thicker posteriorly and ends in a narrow ridge at the base of the arms. This is possibly a luminous organ; as I wished to save the specimen, I did not make sections, but I intend to examine its structure in the more common *Tr. riisei.* In this species, which has a silvery-shining eyeball, I found a very similar thickening on the ventral side. The lid margin is thickened far posteriorly; it has a small, pointed sinus anteriorly toward the base of the arms.

The **arm apparatus** is moderately developed. The arms are rounded in cross section, without sharp edges. Formula: 2, 3, 4, 1. Swimming membranes (keels) are present on all arms, but they differ in form. Those of the 1st arms are restricted to the distal half and project slightly; the 2nd arms bears well developed swimming membranes which become very wide toward the tip and gradually taper toward the base; those of the 3rd arms extend to the base of the arms and widen in the middle; those of the 4th arms extend along the whole arm, surround the base of the tentacles in a curve and continue toward the 3rd arms without passing into the swimming membranes of the third arms.

The protective membranes are well developed and wider at the ventral margin of the arms than at
209 dorsal margin. The ventral protective membranes are supported by long, slender muscular bridges (Plate XXXI, Figure 7); those of the dorsal membranes are short and conical, with a thick base on which the stalks of the suckers rest (Figure 8).

The suckers are largest on the 2nd and 3rd arms, where they are 1 mm wide. Those of the 1st arms are slightly smaller, those of the 4th arms are the smallest. The suckers are cuplike, with narrow

conical stalks which pass into the base of the muscular bridges. The dorsal margin of the larger suckers bears 8 densely arranged, crenelated teeth which are almost perpendicular, become lower toward the ventral margin and pass into a chitinous ring which may be smooth or slightly indented. The suckers usually end some distance from the buccal funnel and leave the arm base free (Plate XXIX, Figure 11).

The **tentacles** (Plate XXXI, Figures 2, 3) are relatively short. Their stalk is flat on the inner side, rounded on the outside, with small suckers on an area of 6 mm near the club. The suckers are single proximally, then 2 rows and then 4 indistinct rows.

The **club** is 3 mm wide; its tip is curved dorsally like a chamois horn and has a large keel (swimming membrane) in the distal half which is displaced dorsally (Figure 2). One of the important characters is the unusually wide club which is caused by the protective membranes with their oblique , dense muscular supports. This applies mainly to the ventral protective membranes, which are almost half as wide as the club.

The number of longitudinal rows of suckers increases from the distal end of the tentacle stalk without forming a well-defined carpal part; there are at first 6, then 8 and finally 14 longitudinal rows. The small suckers remain of about equal size to the middle of the club, then follow 2 or 3 oblique rows of slightly larger suckers and then suddenly much larger suckers of which there are at first 7, then 6 and finally 4 in each oblique row. Toward the tip, there are rows of 4 suckers which become gradually smaller and pass into rows of 3 suckers which are finally displaced ventrally. The rows are curved dorsally at the tip and the suckers become more numerous. The ventral protective membrane bears about 3 longitudinal rows of stalked suckers in the middle of the club, the dorsal membrane a single row of small suckers at the margin. The suckers are situated on a narrow stalk; they are cuplike and bear numerous small denticles on the dorsal side (Plate XXXI, Figure 5).

The club of *Br. riisei* is similar in form but more slender and the proximal half is narrower; its protective membranes bear suckers as in *B. picta.*

The **buccal funnel** (Plate XXIX, Figure 11) is low, almost smooth inside, with 7 pillars, of which the ventral ones are slightly approximated. Membranes of attachment extend from the pillars dorsally to the 1st and 2nd arms and ventrally to the 3rd and 4th arms. There is a distinct short muscle of attachment for the tentacles.

210 The **buccal cone** is high and has a well-developed fluted inner lip; the outer lip forms only a narrow membrane.

The **coloration** is rather intense and has a purplish brown background caused by numerous, densely arranged chromatophores. It is slightly more intense on the dorsal side of the mantle along the gladius, and the dorsal side is usually slightly more intensely pigmented than the ventral side. Chromatophores are almost completely absent on the ventral side of the fins. There are 4 large chromatophores on the dorsal side of the head and 3 on the ventral side. Arms and tentacles are strongly pigmented on the outside but only weakly on the inside, and the chromatophores are regularly distributed on the muscular supports of the protective membranes.

We have already mentioned that the ventral side of the eyes bears club-shaped stripes which are probably luminous organs.

The **gladius** is 35 mm long. Its anterior part is 19 mm and the other 16 mm are occupied by the relatively wide cone (Plate XXXI, Figure 1). It consists of broad wings which converge ventrally and are fused posteriorly into a short, pointed, closed funnel. The rhachis tapers gradually toward the cone: it is enclosed by narrow seams which are the last remnants of the vane and pass into the wings of the cone. The ratio between cone and anterior part is about 4:5, and the relative length of the cone is apparently characteristic for the species.

Mantle complex

(Plate XXXII)

Opening of the mantle cavity (Plate XXXII, Figure 1) shows the normal topography of the liver (*hep.*), the ink sac, which is displaced slightly to the left, the rectum with the anus, the vena cava, which opens in 3 venous sacs (*sacc. v.*) and the rounded branchial hearts (*c. branch.*) with the very long gills. The long caecum (*st. coec.*) and the short stomach (*st.*) are visible through the abdominal wall.

The funnel depressors (*mu. depr. inf.*) are of unusual form. As they are displaced in our specimen by the curvature of the funnel, I refer the reader to Text Figure 1 (p. 5), which shows the condition of *Br. riisei.* They are band-shaped and end posteriorly in narrow processes more or less at the level of the base of the gills; they converge anteriorly so that they are nearly contiguous and accompany the vena cava to the point where it enters the funnel organ. This broad, bandlike form of the depressors of *Brachioteuthis* resembles that in the Chiroteuthidae, in which, however, the depressors are not situated so close together in the middle. As already stated in the introduction (p. 6), this form of the depressors facilitates the understanding of their peculiar modification in the Cranchiidae. STEENSTRUP (1881, p. 294) considered the long, wide funnel depressors as characteristic for the genus *Tracheloteuthis.*

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Intestinal tract

The esophagus (Figures 3, 4, *oes.*) is relatively wide and passes on the right side slightly over the posterior margin of the liver before it opens in the acorn-shaped stomach (*st.*) which is situated on the right side. It is much shorter than the unusually long, sac-shaped caecum (*st. coec.*), which is situated on the left side and has an oblique inner fold on its anterior ventral side from which extend spiral folds. The posterior folds are long and extend almost to the end of the caecum. The caecum ends anteriorly in processes (Figure 4, *st. coec.'*) with weak longitudinal folds. There is a process which projects into the interior in front of the posterior end of the caecum, probably the accidentally invaginated tip of the organ.

Stomach and caecum open in a wide sinus (Figure 4, *sin. st.*), the beginning of the mid-intestine (*int.*), which is curved ventrally behind the liver and then passes into the rectum (*rect.*) which opens between the two anal lips. The anal appendages are small and spatulate.

The ovoid liver (*hep.*) is situated obliquely and is slightly wider anteriorly. Its envelope is not so silvery as in *Br. riisei.*

The large pancreatic appendages (*pancr.*) form compact glandular lobes on both sides, the two anterior lobes, particular the ventral one (*pancr.'*), being larger than the following lobes. The pancreas usually forms two longitudinal rows of lobes which meet at the ventral anterior end of the caecum and open into the latter.

The relatively large **ink sac** (*atr.*) is tubular and situated in the longitudinal axis slightly left of the rectum.

Vascular system

(Plate XXXII, Figure 6)

The vena cava (*v. c.*) passes in the arrow-shaped indentation of the median funnel organ to the ventral surface, then passes on the right near the rectum and opens into a median venous sac (Figure 3,

sacc. v.[1]) on the dorsal side of which the part without venous appendages extends far posteriorly. Before opening into the venous sac, the vena cava receives a large hepatic vein (*v. hep.*). It then branches into two large lateral sacs (Figure 3, *sacc. v.*[2]) which receive on each side the abdominal vein (*v. abd.*) and the mantle veins (*v. pall.*) opening into it. The mantle veins pass in a curve dorsal to the branchial heart.

The branchial hearts (*c. branch.*) are rounded and have a small, knob-shaped appendage on the dorsal inner side. The branchial arteries (*a. branch.*) originate on the branchial hearts. The long branchial veins (*v. branch.*), which contain arterial blood, open into the heart without widening markedly. The very long, slender gills reach to the level of the funnel cartilage; the long mantle cartilages project
212 laterally beyond the anterior end of the gills. The long, bandlike form of the branchial gland is caused by the form of the gills.

The **heart** (*c.*) is spindle-shaped and situated obliquely on the mid-intestine on the right side (Figure 3). It is only slightly produced at the entrance of the branchial veins. The cephalic aorta (*a. ceph.*) ascends dorsally on the right posterior margin of the liver and passes to the right of the esophagus. The posterior aorta (*a. post.*) extends in a curve from the posterior end of the heart and soon branches into the mantle artery (*a. pall.*), which borders the septum anteriorly.

The **renal sac** has two small oval openings at the level of the anterior processes of the pancreas.

Examination of the **genitalia** proved the specimen to be a young male; its small, more or less triangular testis (Figure 3, *test.*) is situated near the dorsal posterior margin of the stomach and is attached to the dorsal posterior side of the body by the long gastrogenital ligament (*lig. g. g.*). The gonoduct, situated behind the left branchial heart, was in an early stage of development.

Measurements of *Brachioteuthis picta*

Dorsal length of mantle	35 mm
Width of mantle margin	7.5 mm
Width of middle of mantle	5.5 mm
Length of fin	18 mm
Width of both fins	18 mm
Width of head	7.5 mm
Length of head	7 mm
Length of 1st arm	9 mm
Length of 2nd arm	17 mm
Length of 3rd arm	15 mm
Length of 4th arm	12 mm
Length of tentacles	23 mm
Length of club	9 mm
Width of club	3 mm

Juvenile forms of *Brachioteuthis*

At three stations we found young Oegopsida which certainly belong to the developmental cycle of *Brachioteuthis*. I shall start with the description of a particularly well-preserved juvenile stage from

the Indian South Equatorial Current (Station 236). That this specimen belongs to *Brachioteuthis* is hardly evident at first glance (Plate XXX, Figures 2 and 3). It has a dorsal mantle length of 5.5 mm and a reddish brown pigmentation which is stronger on the entire dorsal side than ventrally.

The goblet-shaped **mantle** is rounded posteriorly and has a distinctly projecting dorsal corner and more weakly projecting ventral corners. The semicircular terminal fins are not pigmented; they are 1.8 mm long, which is barely one third of the mantle length. Both fins together are 2 mm wide. They do not project beyond the posterior end of the body and are separated dorsally by a wide space.

213 The **head** is short and wide, with large but not markedly protruding eyes. There are slight indications of neck folds, of which the middle fold bears the knob-shaped olfactory tubercle. The arm formula is 2, 1, 3, 4; the 1st and 2nd arms are about equally 3 mm long.

The **tentacles** are 6 mm long and the club is markedly widened (Plate XXXI, Figure 4). The tentacle stalk has a flattened inner side and bears a few small suckers in a row which pass from the ventral to the dorsal side in the distal part. The club bears two weakly developed protective membranes and numerous densely arranged suckers which become gradually smaller toward the tip. There is no marked difference in the size of the suckers on the broad side of the club. They form numerous rows (about 9); only the suckers at the tip are arranged in quadriserial rows.

It is important for the determination of the systematic position of the larva that a club of this form occurs only in the Tracheloteuthidae and Histioteuthidae. The larva does, however, not belong to the Histioteuthidae for the following reasons:

1. The mantle is goblet-shaped, not sac-shaped, as in the larvae of Histioteuthidae.
2. The fins of the larvae of Histioteuthidae are situated obliquely and project beyond the posterior end of the body, where they become fused. The fins of this larva do not project beyond the posterior end of the body and are contiguous only at the posterior end of the body.
3. The larvae of Histioteuthidae have no neck folds.
4. Larvae of Histioteuthidae of the same size already have well-developed luminous organs which appear at an early stage of development and are absent only in the youngest stages.
5. The chromatophores of this larva are much more numerous than in the larvae of Histioteuthidae.

The larva therefore probably belongs to the developmental cycle of *Brachioteuthis*. If this proves correct, the intense pigmentation would indicate *Brachioteuthis beanii* or *Br. picta*; but it is also possible that it belongs to a new species.

We caught the single larva at Station 236 (4°38′ S, 57°16′ E) in the Indian South Equatorial Current.

Measurements

Dorsal length of mantle	5.5 mm
Width of mantle	2 mm
Width of both fins	2 mm
Length of fins	1.8 mm
Length of 1st arm	3 mm
Length of 2nd arm	3 mm
Length of 3rd arm	2.7 mm
Length of 4th arm	2.3 mm
Length of tentacles	6 mm

214 Another larva (Plate XXX, Figure 1) differs distinctly in habitus from the above larva and is about twice as large, 20 mm long. This larva resembles the larva described by Hoyle (1886, *Chall. Ceph.*, p. 166, Plate 31, Figures 6–10). Hoyle placed his larva, with some reservation, in the developmental cycle of *Brachioteuthis*; I fully agree, because the larva shows characters which are present only in this genus.

The **mantle** has a dorsal length of 11 mm; it is broadly goblet-shaped and has a pointed posterior end. The dorsal corner projects markedly, the ventral corners are barely distinguishable.

The **fin** is heart-shaped and 2.3 mm long, barely one quarter of the mantle length. It does not project beyond the posterior end of the mantle but tapers sharply toward the pointed posterior end.

The **funnel** is of medium size; its opening is curved slightly downward and projects beyond the mantle margin. Particularly characteristic is the long, slender neck which resembles that of the Chiroteuthidae. The head is differentiated sharply from the neck; it is rounded because of the large optic ganglia. The relatively small eyes show no distinct sinus on the lid margin. The olfactory tubercle is barely visible as a small knob, and folds are completely absent.

The **arm apparatus** is still little developed, except for the large tentacles. The arm formula is 3, 2, 1, 4. The 1st arms bear only two distinct suckers; the other arms bear a large proximal sucker, followed by 3 pairs of suckers of decreasing sizes.

The **club** (Plate XXXI, Figure 6) is slender, only slightly widened, still without membranes. Since the proximal suckers belong to the tentacle stalk, the sucker-bearing area forms nearly two thirds of the length of the tentacle. The suckers are arranged so that two marginal rows extend from one proximal sucker. Between the marginal rows are two other rows which also extend from a single sucker and pass into the normal rows of 4 suckers. There are additional rows of suckers near the tip, so that there are 5, 6 and finally 7 rows. The suckers become smaller distally and suddenly very small and dense at the tip.

This arrangement of the rows of suckers is present only in *Brachioteuthis*; all proximal rows of 2 or 4 suckers belong to the tentacle stalk; the following suckers belong to the hand part, which becomes more distinctly differentiated later.

The habitus of the larva resembles so closely that of the Chiroteuthidae that it could be placed in this family. However, the larva does not belong to *Chiroteuthis* because there are more than 4 rows
215 of suckers in the distal half of the club. Moreover, larvae of *Chiroteuthis*, i.e. *Doratopsis*, of similar size have distinct olfactory tubercles with a long stalk, and their ventral arms are large.

There thus remains only the genus *Brachioteuthis*, in which Hoyle and Pfeffer already placed a number of similar larvae, especially those described by Rochebrune (1884, p. 15; Plate II, Figures 7–11) as *Entomopsis*. Our larva definitely belongs to *Brachioteuthis* because of the form of the mantle complex. Opening of the mantle cavity shows the broad, band-shaped funnel depressors which closely resemble those of *Brachioteuthis riisei*. The visceral complex is restricted to the posterior quarter of the body as in *Br. riisei*, in which the posterior displacement of the visceral complex was observed already by Steenstrup (1881, p. 294). The mantle cavity of *Br. riisei* (Text Figure 1, p. 5) closely resembles that of this larva, and funnel and cartilages are also similar.

The fact, moreover, that the larva is only weakly pigmented and that the head bears the characteristic large chromatophores which are typical for *Br. riisei* removes any doubt in my mind that it can be placed in the developmental cycle of *Br. riisei*.

Our larva was caught on the West African coast at Station 66 (3° 55′ S, 7° 48′ E) in the northern branches of the Benguela Current, in a vertical net.

I have a much younger stage from the Indian South Equatorial Current (Station 237). This larva has a very strange form (Plate XXIX, Figures 9, 10) and it is difficult to believe that it does indeed

belong to the developmental cycle of *Brachioteuthis*. However, it obviously resembles the large larva described above. The larva has a dorsal mantle length of 4 mm, a broad, sac-shaped mantle and small fins at the posterior end. Its funnel also projects beyond the anterior margin of the mantle; especially striking is the long neck, which resembles that of a camel and bears a pear-shaped head with relatively small eyes.

The **arm apparatus** is very little developed, except for the flaglike tentacles; the 3rd and 4th arms form only short stumps. The 1st and 2nd arms bear only one sucker.

The **tentacles** are covered with suckers on the inner side for three quarters of their length. The suckers start out in 2 rows, passing to 3 rows in the distal part. The long, band-shaped funnel depressors are visible through the mantle.

We have also another stage from Station 88 in the Benguela Current which closely resembles that described by HOYLE. The neck and funnel of this specimen are completely retracted into the large, sac-shaped mantle, which is 12 mm long. However, the arms are less developed than in the large larva described above.

216 # 8. Family **Chiroteuthidae** Gray, 1849

The family Chiroteuthidae was established by Gray (*Catalogue of the Mollusca*, 1849, p. 42) for the genera *Chiroteuthis* and *Histioteuthis*, which were discovered by Vérany and were described by Férussac (1834).

Gray (p. 37) established the families Cranchiadae and Loligopsidae for the other deep-sea Cephalopoda which have no hooks on the arms.

Steenstrup (1861, p. 69) gave a more exact definition of the "Cranchiae." He united the two families of Gray under the name of Cranchiaeformes as opposed to all other deep-sea forms with suckers which he named Taonoteuthi. Steenstrup did not give an exact definition of his Taonoteuthi, and we must refer to other specialists who attempted to do this in the sense of Steenstrup and apparently under his personal influence.

The composition of the Taonoteuthi presented below is that of Hoyle ("*Challenger*" *Report*, 1886, p. 42):

Taonoteuthi Steenstrup (1861, p. 69)

Subfamily Chiroteuthida	*Chiroteuthis* d'Orbigny, 1839
	Histiopsis Hoyle, 1885
	Calliteuthis Verrill, 1880
	Brachioteuthis Verrill, 1881
	Doratopsis De Rochebrune, 1884
	Histioteuthis d'Orbigny, 1839.

This list contains all deep-sea Cephalopoda known at the time which have suckers on arms and tentacles. Hoyle does not give any definition of the Taonoteuthi, and I know of no other character which could be applied to all the genera listed, except the gelatinous consistency of the body—a phenomenon of convergence which occurs in very different groups. Other specialists also maintained the group "Taonoteuthi" but again gave no definition. It is not surprising, therefore, that attempts were made to divide the group into a number of families. Verrill (1881, p. 430) divided the Taonoteuthi into the following three families without regard to the relationship among the genera:

Chiroteuthidae restr.	*Chiroteuthis* d'Orbigny *Brachioteuthis* Verrill, 1881 *Calliteuthis* Verrill, 1881
217 Histioteuthidae fam. nov.	*Histioteuthis* d'Orbigny
Mastigoteuthidae fam. nov.	*Mastigoteuthis* Verrill, 1881

This classification shows that Verrill did not recognize the close relationship between *Histioteuthis* and *Calliteuthis* and that his Chiroteuthidae include completely heterogeneous forms. These errors in Verrill's classification, together with his inclination to make an excessive number of divisions into families, explain that neither Jatta (1886, pp. 40 and 107) nor Joubin (1900) accepted his classifica-

tion. Both authors maintain the group "Taonoteuthi", Joubin (1900, p. 88) giving the following composition of the group on the basis of recent data:

Family Taonoteuthidae:

Subfamily Chiroteuthinae: without luminous organs	*Grimalditeuthis* Joubin, 1900 *Chiroteuthis* d'Orbigny *Brachioteuthis* Verrill, 1881 *Entomopsis* De Rochebrune, 1884 *Doratopsis* De Rochebrune, 1884
Subfamily Histioteuthinae: with luminous organs	*Calliteuthis* *Histiopsis* *Histioteuthis*

Again, a definition of the Taonoteuthi is not given, but the subfamilies are defined. Collection of the genera *Calliteuthis*, *Histiopsis* and *Histioteuthis* under one group could be accepted, but a classification based on the presence of luminous organs is not justified because these are also present in the Chiroteuthinae.

Of all attempts to give a natural classification of the Taonoteuthi, the system proposed by Pfeffer (1900) seems the most acceptable; it has so many advantages that Hoyle (*Genera rec. dibranch. Cephalopoda*, 1904, p. 3) accepted it in many points.

Pfeffer divided the Chiroteuthidae and related forms into the families Chiroteuthidae and Grimalditeuthidae, with the following genera:

Chiroteuthidae Gray, 1849	*Doratopsis* Rochebrune, 1884 *Chiroteuthis* d'Orbigny, 1839 *Chiroteuthopsis* Pfeffer, 1900 *Mastigoteuthis* Verrill, 1881
Grimalditeuthidae Pfeffer, 1900	*Grimalditeuthis* Joubin, 1898

In my opinion, however, the Grimalditeuthidae and the Chiroteuthidae are so closely related that
218 they should be united. The resemblance of the posterior end of the body of *Ch. macrosoma* and *Ch. imperator* and of *Grimalditeuthis* is so striking that it cannot be ignored. Pfeffer recognized this and stated that the Grimalditeuthidae could also be placed as a subfamily in the Chiroteuthidae, "but this would cause such marked changes in the definition of the family that only the characteristic gladius would remain as a character and this is present also in the Cranchiidae." Before entering into this controversy, we give a diagnosis which applies to all Chiroteuthidae, including *Grimalditeuthis*.

Chiroteuthidae

Body gelatinous; mantle long, goblet-shaped, with pointed posterior end. Fins large, head long, neck without folds; olfactory tubercle stalked. Funnel with valve; funnel adductors not visible externally. Funnel depressors band-shaped, broadly diverging posteriorly, margins of funnel, collaris and funnel depressors not fused with the mantle. Arm apparatus well developed; arms with two rows of suckers, clubs with 4 or more rows of suckers; tentacle stalk without suckers; 4th arms attached ventrally. Gladius with weakly developed vane and a long cone.

Chiroteuthidae { **Chiroteuthinae** / **Mastigoteuthinae** / **Grimalditeuthinae**

PFEFFER maintains that the inclusion of the genus *Grimalditeuthis* in the Chiroteuthidae would make it impossible to distinguish between them and the Cranchiidae. Attention should be paid, therefore, to the following important differences, some of which are included in the above definition. The narrow fins of the slender Cranchiidae whose gladius has a cone, as the genus *Taonius*, form an oblong oval and there is never a delicate accessory fin behind them, like that in *Grimalditeuthis* and in the subgenus *Chirothauma*. However, the differences in the funnel are more important: it has a valve in all Chiroteuthidae, including *Grimalditeuthis*, while a valve is absent in all Cranchiidae.

The genus *Grimalditeuthis* resembles the Cranchiidae in the ventral fusions between the mantle and funnel cartilages but it differs from them in that there is no fusion of the neck cartilage. Moreover, such fusions on the ventral margin of the mantle are occasionally present also in closely related genera, e.g. *Symplectoteuthis* in the Ommatostrephidae and *Sepiadarium* in the Myopsida. These fusions, however, never produce the characteristic concrescences of the mantle with the funnel depressors, the margins of the collaris and the funnel which is typical for the Cranchiidae. In his description of *Grimalditeuthis* JOUBIN stressed the transparency of this beautiful form; he would surely also have mentioned the distinct stripes of fusion on the mantle, had they been present.

219 I therefore believe that my definition of the Chiroteuthidae contains sufficiently sharp distinctions from the Cranchiidae.

I divide the Chiroteuthidae into three subfamilies, as follows:

a) Mastigoteuthinae

Fins terminal, rhomboidal or heart-shaped; posterior end of body slightly produced, very narrow. Funnel small; funnel cartilage oval or ear-shaped, often with a tragus, sometimes also with an antitragus. Mantle cartilage noselike. Head of moderate length; olfactory tubercle with a short stalk. Eyeball without luminous organs. Arm apparatus of medium development, ventral arms longer than the other arms.

Tentacles whiplike, without glandular knobs; club long, not widened. Suckers on tentacles small, numerous, arranged in oblique rows. Luminous organs numerous and scattered on the body, or forming groups of two at the eye sinus, or absent.

Caecum and stomach of equal length. Branchial hearts situated far from base of gills, branchial arteries long. Ink sac not covered by ventral luminous organs.

b) Chiroteuthinae

Fins circular; posterior end of body ending with the fins or projecting beyond them and in this case surrounded by a separate accessory fin membrane. Funnel small; funnel cartilage ear-shaped, with tragus and antitragus. Mantle cartilage noselike, with grooves into which tragus and antitragus fit. Head long, cylindrical or rounded; olfactory tubercle with a long stalk. Eyeball large, with luminous stripes or with luminous organs in rows on the ventral side. Arm apparatus strongly developed. Ventral arms longer than the other arms, with wide swimming membranes and with luminous organs in one row.

Tentacles whiplike, very long, with glandular knobs on the outer side. Clubs with wide protective membranes, with a large glandular knob at the end; suckers on club helmet-shaped, with long stalks and forming quadriserial rows.

Caecum smaller than stomach; ink sac broad, heart-shaped, covered by two large luminous organs.

c) Grimalditeuthinae

Fins transverse oval; posterior end of body projecting markedly beyond the fins and surrounded by a delicate, heart-shaped accessory fin. Funnel large, reaching to the eyes. Funnel cartilages and mantle cartilages absent, replaced by a broad fusion of funnel and mantle margin. Neck cartilage present. Head long, cylindrical; olfactory tubercle with a long stalk. Eyes not protruding; arm apparatus of medium development, all arms ending in knoblike pigmented swellings. Ventral arms not longer than the other arms. Tentacles unknown; luminous organs absent.

220 Under my division, each of these subfamilies consists of a single genus:

1. The Mastigoteuthinae consist only of the genus *Mastigoteuthis*. Pfeffer added another genus *Chiroteuthopsis*. However, it resembles *Mastigoteuthis* so closely in all important characters that I suggest to consider it as a synonym of *Mastigoteuthis*.

2. The Chiroteuthinae consist of the genus *Chiroteuthis*. Pfeffer and Hoyle added *Doratopsis* as a separate genus. For reasons shown below, I agree however with Ficalbi, who considered the species of *Doratopsis* as juvenile forms of *Chiroteuthis*.

3. Pfeffer places *Loligopsis bonplandii*, established by Vérany in 1837, in the Grimaldoteuthinae Although this species apparently differs distinctly from *Grimalditeuthis richardii* Joubin in that the former lacks a posterior fin, I agree with Pfeffer that the two are identical and the apparent differences are due to a damaged posterior end. The Grimalditeuthinae thus contain only the single species *G. bonplandii*.

1. Subfamily: *Mastigoteuthinae*

Mastigoteuthidae Verrill, 1881, p. 430.
Mastigoteuthidae Hoyle, 1886, p. 36.
Taonoteuthi Joubin, 1895, p. 38.
Chiroteuthidae Pfeffer, 1900, pp. 184, 187.
Taonoteuthi subf. Chiroteuthidae, Fischer and Joubin, 1906, p. 342.

Mastigoteuthis Verrill, 1881

Mastigoteuthis agassizii Verrill, 1881, *"Blake" Rep.*, p. 100, Plate I, Figure 1; Plate II, Figures 2, 3–3g.
Mastigoteuthis agassizii Verrill, 1881, *N. Am. Ceph.*, p. 297, Plate XLVIII; Plate XLIX, Figures 2, 3–3g.
Mastigoteuthis agassizii Hoyle, 1886, *"Challenger" Rep.*, p. 170, Plate XXIX, Figures 8–10.
Chiroteuthis bomplandi (?) Joubin, 1893, *Oeil thermoscopique*, p. 1, Figure.
Chiroteuthis grimaldii Joubin, 1895, *Camp. Scient. Monaco*, p. 38, Plate III, Figures 1–4; Plate IV, Figures 1, 2; Plate V, Figures 2, 4–9, 12.
Mastigoteuthis levimana Lönnberg, 1896, *Some Rare Ceph.*, p. 605.
Mastigoteuthis agassizii, levimana, 1900, Pfeffer, *Syn. Oegops.*, p. 187.
Chiroteuthis? sp.? Joubin, 1900, *Camp. Scient. Monaco*, p. 89, Plate X, Figure 13; Plate XIV, Figure 7–9.
Mastigoteuthis dentata Hoyle, 1904, *"Albatross" Rep.*, p. 34, Plate VI, Figure 8–11.

Chiroteuthis talismani, Ch. grimaldii Fischer and Joubin, 1906, *Exp. "Travailleur" et "Talismani"*, p. 342, Plate XXV, Figures 1–4; p. 345, Plate XXV, Figures 5–8.

Mastigoteuthis cordiformis, M. flammea, M. glaucopis Chun, 1908, *Ceph., Deut. Tiefsee-Exp.*, p. 88.

Mastigoteuthis

The genus *Mastigoteuthis* was established in 1881 by Verrill, who described two specimens caught by the *Blake* south of Cape Hatteras as *M. agassizii.*

221 Our knowledge of this interesting genus was increased by Lönnberg (1896), who described two damaged specimens from the stomach of a dolphin as *M. levimana.* These specimens had no clubs; however, the clubs were described by Verrill and also by Hoyle in the "*Challenger*" *Report.* The fragments described by Hoyle were from near Teneriffe. Joubin (1900) also described and illustrated a club collected near the Azores on a cruise of the *Prince of Monaco.* He did not realize that the club belonged to *Mastigoteuthis*, but he noted that the suckers resembled those of the Chiroteuthidae.

Joubin (1895) described *Chiroteuthis grimaldii*, which also belongs to *Mastigoteuthis.* With these records, the state of knowledge on the genus *Mastigoteuthis* at the end of the century is summed up.

Considerable progress has been made since. Hoyle (1904) described a larger Pacific species, *M. dentata*, caught by the *Albatross* in the Gulf of Panama and near the Galápagos islands. Fischer and Joubin (1906) described two smaller species from the Atlantic, *Chiroteuthopsis talismani* (south of the Azores) and *Ch. grimaldii* (coast of Morocco). Three well-characterized new forms from the catch of the German Deep-Sea Expedition, which I described briefly (1908) as *Mastigoteuthis cordiformis* (Nias Canal near Sumatra), *M. flammea* (Guinea Current) and *M. glaukopis* (coast of East Africa), can now be added.

Our material is so well preserved that it makes a revision of the generic diagnosis possible. Pfeffer (1900) gave the following diagnosis: "Locking cartilage of funnel without tragus or antitragus; cartilaginous groove and locking cartilage of mantle rounded triangular; tentacles without swollen clubs, with numerous rows of very small suckers; buccal membrane with 6 points."

The following can be added to the above diagnosis. In *M. flammea* and *M. cordiformis*, a tragus and an antitragus are well developed on the funnel cartilage (Plate XXXV, Figures 1, 3). The antitragus is liable to be overlooked at first sight; however, it is distinctly visible if the funnel cartilage is examined more closely under the binocular microscope, in good light.

M. glaukopis has no antitragus but has a distinct tragus (Figure 2). I therefore assume that similar conditions are present also in the other species and that tragus and antitragus have been overlooked. Fischer and Joubin also noted (p. 344) that the groove of the funnel cartilage of *Chiroteuthopsis talismani* apparently contains a tragus.

As to the statement "buccal membrane with 6 points", there are 7 points in all specimens examined. The ventral points, although closely approximated, are distinctly separated (Plate XXXV, Figures 8, 9).

Thus, the only character that justifies a generic distinction from *Chiroteuthis* is the form of the
222 club. In fact, the club of *Mastigoteuthis* is so peculiar and differs so markedly from those of the other Chiroteuthidae that fragments of tentacles can be identified with certainty as belonging to this genus. The club is preserved in *M. cordiformis*, which has a tragus and an antitragus, and in *M. glaukopis*, which has only a tragus.

According to Pfeffer's definition, *M. glaukopis* should be placed in *Chiroteuthopsis.* He gives the following diagnosis for this genus: "Locking cartilage of funnel with tragus but without antitragus; end of gladius ending at the level of the posterior margin of fin, which is short and pointed."

Pfeffer established the genus *Chiroteuthopsis* for *Chiroteuthis grimaldii* Joubin, the tentacles of which were lost. Since the well-preserved club of my specimen shows in every respect the characters of the genus *Mastigoteuthis*, *Chiroteuthopsis* should be considered as a synonym of *Mastigoteuthis*. A minor and variable character like the absence of an antitragus does not justify the establishment of a new genus. After the inclusion of the species described by Joubin in *Mastigoteuthis*, the diagnosis of this genus is as follows.

Mastigoteuthis

Locking cartilage of funnel ear-shaped, with a tragus, sometimes also with an antitragus. Locking cartilage of mantle noselike, with pitlike depressions for the tragus or antitragus. End of gladius at pointed posterior margin of fin. Ventral arms longer than the other arms. Buccal membrane with 7 points; tentacle whiplike, without swelling of club; club long, without swimming membrane, with weakly developed protective membranes; suckers very small, gradually decreasing in size distally and forming very numerous oblique rows, each with 20–30 suckers.

The following key can be used for determination of the 6 species of *Mastigoteuthis* known to date.

223 Key to the Species of *Mastigoteuthis*

- Fins rhomboidal or eliptical, half as long as mantle or shorter.
  - Suckers present along whole length of ventral arms.
    - Numerous luminous organs (with an external chromatophore) scattered all over the body.
      - Suckers of arms with smooth margin. Tragus and antitragus not demonstrated. *M. agassizii* Verrill
      - Suckers of arms with long denticles on dorsal margin. Funnel cartilage with tragus. Eyes protruding. *M. grimaldii* Joubin
      - Suckers of arms with a few small denticles. Funnel cartilage with tragus and antitragus. Eyes small, not protruding. *M. flammea* Chun
    - Two luminous organs on ventral margin of eye sinus.
      - Suckers of arms with blunt, conical denticles. Funnel cartilage with tragus. Eyes large. *M. glaukopis* Chun
    - Luminous organs absent.
      - Fins of male 2/3 of mantle length, fins of female 2/5 of mantle length. Suckers of arms with sharp denticles on dorsal margin. *M. dentata* Hoyle
  - Suckers few and restricted to base of ventral arms.
    - Suckers of arms with wide, crenelated denticles. Tragus and antitragus not demonstrated. *M. levimana* Lönnberg
- Fins heart-shaped, large, three quarters of mantle length.
  - Suckers present along whole length of arms.
    - Eyes large, protruding. Head wide. Suckers of tentacles with large, steeply projecting denticles. Funnel cartilage with tragus and antitragus. Body covered with small, conical tubercles. *M. cordiformis* Chun
  - Suckers restricted to base of all 8 arms.
    - Eyes small. Head narrow. Body smooth. Funnel cartilage with tragus. *M. talismani* Fischer and Joubin

Mastigoteuthis cordiformis Chun

Mastigoteuthis cordiformis Chun, 1908, p. 88.

(Plate XXXIV, Plate XXXV, Figures 1, 5, 6, 8, 10–14; Plate XXXVI, Figures 3–5; Plate XXXVII, Figure 5).

Locality: Station 194; south of Pulo Nias (Sumatra). Indian Counter-current, 0° 15′ N, 98° 8′ E. Trawl 614 m—One male.

I have an almost intact specimen of this relatively large species with both tentacles well preserved. The body is gelatinous, with unusually large fins. The head is wide and has large eyes. The arm apparatus is not unusually large.

224 The **mantle** is conical, with a narrow posterior part which ends in a point about 9 mm long. Ventral and dorsal corners of the mantle project only slightly. Dorsal mantle length: 83 mm.

The **fin** is very large in comparison with the mantle. It is heart-shaped, narrows toward the posterior end of the body and surrounds it with weak seams. Each half of the fins is 65 mm long and both fins together are 60 mm wide. The fin thus occupies more than three quarters of the mantle length, which is not the case in other species of *Mastigoteuthis*.

The **funnel** is of medium size and reaches to the lower third of the eyes. It has a valve and a funnel organ of normal form which consists of a middle part with a sharp margin that forms two long posterior processes and of two lateral bluntly rhomboidal parts.

The funnel adductors do not project externally and are visible only indistinctly through the skin. However, the funnel depressor is more distinctly delimited from its surroundings than in *Chiroteuthis*.

The **head** has a short neck and is 28 mm wide, like the maximal width of the mantle. This large size of the head is caused by the large, slightly protruding eyes. The right eyeball of the preserved specimen protruded, so that it could be measured; it was both 13 mm long and wide. The lens is free for a width of 5.5 mm. A groove was distinct on the left eye, which was not protruding.

The border between head and neck is indicated by a not very sharply defined transverse gelatinous swelling in the form of two cheeks which surround the shallow funnel groove with its adductors which are visible, shining through. This swelling passes dorsally into an indistinct swelling. The knob-shaped olfactory tubercle with a short stalk projects between the two swellings.

The funnel cartilage (Plate XXXV, Figure 1) is ear-shaped, widened posteriorly, with a sharp, thin cartilaginous margin which is higher anteriorly (Plate XXXVI, Figure 3). The tragus is well developed and much larger than the small antitragus. The groove of the cartilage is divided posteriorly.

The mantle cartilage resembles a nose which passes gradually anteriorly into the mantle surface. It fits exactly inside the funnel cartilage, so that there is a corresponding depression for the tragus and antitragus.

The neck cartilage (Plate XXXVI, Figure 5) is spatulate, slightly concave laterally and with a median groove bordered by two longitudinal ridges. The opposite cartilage on the inner dorsal margin of the mantle bears a longitudinal median ridge and weakly developed marginal ridges.

The **arm apparatus** is moderately developed. Arm formula: 4, 2, 3, 1; the ventral arms are the longest, 60 mm long. All arms bear narrow protective membranes which are supported by wide muscular bridges; distally the protective membranes gradually disappear.

225 The swimming membranes form weakly developed keels, which are barely visible on the first 3 pairs of arms and slightly more distinct on the ventral arms.

The suckers are not markedly smaller on the ventral arms than on the other arms; there are 57–

59 pairs on the ventral arms and 50 on the 3rd arms. The stalks of the suckers widen into conical pads which are situated on the muscular supports of the protective membrane in the distal part. They are acorn-shaped in side view (Plate XXXV, Figure 13). The distal margin of the opening (Figure 14) bears blunt denticles which look like indentations. There are small tubercles around the denticles.

Both **tentacles** (Plate XXXV, Figures 8, 10) are well preserved. Their cylindrical stalk is relatively short; the club is not widened and is 61 mm long. There is a narrow, undulate protective membrane on each side of the suckers, supported by short, regularly arranged muscular bridges. The suckers of the tentacles are small and decrease gradually in size toward the tip. Each of the 5 proximal oblique rows consists of two suckers, the following oblique rows of 3 suckers; then follow oblique rows with an increasing number of suckers, up to 25 in the middle of the club. The suckers of the median longitudinal rows are usually slightly larger than the lateral ones; in the middle of the club there are about 3 rows, the suckers of which are slightly larger than those of the lateral rows of the club. The outer side of the tentacle, which is without suckers and has no swimming membrane, narrows distally, probably because of the increase of the number of rows. The rows of suckers are contiguous at the tip, while the free outer side is about as large as the sucker-bearing inner side in the proximal part.

The suckers of the tentacles (Figure 11, 12) have long stalks; they are cup-shaped, 0.5 mm wide and not much longer than wide. Their opening is surrounded by a thick chitinous ring with denticles all around. The dorsal denticles are very long; they are upright on the opening, a unique condition in the Chiroteuthidae. A ring of short, pointed, conical denticles surrounds the chitinous ring of denticles (Figure 12); it is slightly wider dorsally than on the ventral side and ends towards the outside in a very narrow margin of radially arranged chitinous rods.

These suckers differ from those illustrated by Joubin (1900, Plate XIV, Figures 7–9) in that the denticles are upright and also present on the ventral margin. The same applies to the suckers of the tentacles described by Hoyle (Plate XXIX, Figures 8–10) from the fragments found by the *Challenger* expedition. According to Verrill (p. 298, Plate XLIX, Figure 3 e), the suckers of the tentacles of *M. agassizii* are very small and have only 2 or 3 sharp denticles.

The **buccal membrane** (Plate XXXV, Figure 8) shows 7 distinct points, because the two ventral points are separated and supported by two separate pillars. This character is important because Pfeffer mentions only 6 points in the diagnosis of the genus *Mastigoteuthis* (1900, p. 184). This statement of Pfeffer is apparently based on Lönnberg's data (p. 608) on *M. levimana.* However, Verrill (Plate
226 LXIX, Figure 2) shows the buccal membrane of *M. agassizii* with 7 points. This is certainly the normal condition, because the other species of *Mastigoteuthis* also have a buccal membrane with 7 points.

The buccal funnel of *M. cordiformis* is smooth on the outside and shows few chromatophores; but the inner side is light-colored and wrinkled. An outer lip of the buccal cone was not recognizable, but there is a markedly swollen, fluted inner lip. The delicate attachment is as in all Chiroteuthidae.

The **gladius** (Plate XXXV, Figures 5, 6) is 83 mm long and 2.5 mm wide at the anterior end, then widens to 6 mm in the middle and ends in a long, pointed cone. It consists of a flat rhachis, bordered by two submedian ribs which extend toward the cone and end in a shallow keel. The vane is absent at the anterior end; it is then weakly developed and finally forms wide wings posteriorly, which curve ventrally and form the rounded cone. This remains open for some distance, but is closed at the pointed posterior end. As visible in an optic longitudinal section of the gladius in lateral view, the chitinous layer of the rhachis and of the base of the vane thickens at the point where the wings are curved toward each other to form the cone. This thickening disappears toward the closed posterior end of the cone.

Comparison of the gladius with previous descriptions shows the following differences: The gladius of *M. levimana* as described by Lönnberg is much narrower anteriorly, very thin in the middle and

abruptly widened posteriorly. According to VERRILL, the gladius of *M. agassizii* has a relatively plumper cone, and the vane almost disappears in its middle.

The posterior end of the cone of *Mastigoteuthis* contains a few incomplete transverse septa; they will be described later, in connection with *Chiroteuthis*.

The **coloration**, pale flesh-pink, is caused by small chromatophores, which are scattered all over the body, including fins, arms, and tentacles, and are generally denser on the dorsal side. The outer side of the arms and tentacles shows more numerous chromatophores than the inner side. There are also a few larger, and more reddish brown chromatophores at some points.

The entire body of *M. cordiformis* is densely covered with very small **tubercles**, which are visible under the magnifying lens. I examined them carefully because I thought at first that they were small luminous organs. However, their fine structure refutes such an interpretation.

Sections (Plate XXXVII, Figure 5) show that they are conical humps, covered with epithelium (*ep.*). However, on the top of these humps the epithelial cells were always worn off, and only at the base they were well preserved, as shown in Figure 5. The tissue which forms these humps consists of systems of
227 fibers arranged radially to the outer surface and concentrically near the top. They contain large, light-colored cells at the base, with irregular oblong or indented nuclei. They are situated in a liquid cell content of string-like branched plasma. The cells become flat, but their nuclei are distinct, of irregular form, or disc-shaped near the top. Beneath the humps there are chromatophores (*chr.*) and the gelatinous layer of the cutis.

These conical humps are obviously a modified subcutaneous connective tissue which is probably not phosphorescent. However, only examination of the live animal could give information on their function.

Inner Organization

(Plate XXXVI, Figures 3, 4)

My studies of the anatomy of *M. cordiformis* were restricted by the desire to save the only available specimen. However, some characters of the inner organization may be mentioned.

Opening of the mantle from the ventral side shows a posteriorly displaced, thin septum which connects the mantle and the abdominal wall in the middle. It is thin and transparent and contains distinct longitudinal muscular cords which I name "musculus rectus abdominis". This muscle is thicker in front of the renal sacs and then extends broadly in the middle of the abdominal wall, forming two branches around the rectum.

The posterior margin of the funnel is situated above the anus and passes laterally into the sharply separated funnel depressor (*mu. depr. inf.*). The anal appendages are slender and slightly curved. The rectum passes on the median side of the liver and is only slightly differentiated from the mid-intestine, which disappears in the area of the renal sacs. **Stomach and caecum** are distinctly visible through the transparent abdominal wall. Exposure of these organs shows an important character of the genus *Mastigoteuthis*: the large caecum (*st. coec.*), which is nearly as large as the stomach (*st.*). The spiral swelling, from which radiate dense spiral folds (*rad.*), is visible on its left anterior side. The folds are present only on its anterior part, leaving the long posterior part free. The stomach is broadly connected with the caecum and also consists of a muscular middle part (*st.*) with a thin-walled terminal sac (*st.'*). Behind the opening of the esophagus into the anterior part of the stomach, the rounded gastric ganglion (*g. gastr.*), is distinctly visible, with thicker branches radiating from it.

228 **Vascular system**. The vena cava passes on the right side and bears a long complex of venous appendages in the area of the renal sacs. These appendages are distinctly divided posteriorly, while they

gradually become fused anteriorly. The renal sac, which encloses the venous appendages, opens in a pair of chimney-shaped papillae (*ur.*) situated in the middle of the gills. Lönnberg (p. 607) mentions similar papillae in *M. levimana.* Close behind the papillae are the rounded, distinct branchial hearts, which are situated far from the base of the gills in this genus. The branchial arteries (*a. branch.*) are therefore relatively longer than in other Oegopsida and extend in a curve to the base of the gills.

The gills are large and almost reach to the mantle margin; the branchial gland extends to near the mantle cartilage. The gills consist of 27 lamellae, of which the outer are much smaller than the inner ones. The branchial veins are also relatively long.

The abdominal veins (*v. abd.*), and the large pallial veins (*v. pall.*), are distinct. They become thinner posteriorly and form two branches which become united into a vein that passes on the dorsal side of the gelatinous tissue inside the cone. Also distinct is the gastric vein (Figure 4, *v. g.*), which passes at the border between stomach and caecum, and receives several venous branches. The gastric vein descends dorsally and passes into the gastrogenital ligament at the border between the two parts of the stomach. It receives here at first a venous branch from the genital gland and ends in a branch which passes to the dorsal side of the mantle and extends anteriorly in the median line. The gastric vein has only a thin branch in the widened part of the genital ligament (*lig. g. g.*).

The specimen is a young male with as yet immature genitalia—a circumstance due to which a special character of the genus *Mastigoteuthis*, which I found also in the other specimens, could be observed.

The juvenile **testis** is situated entirely on the beginning of the gastrogenital ligament, without touching the stomach. It is 5 mm long and forms a narrow band on the ventral side of the ligament. This is a characteristic difference from *Chiroteuthis*, in which the testis is situated half on the stomach and half on the gastrogenital ligament. In *Mastigoteuthis*, this ligament broadens immediately behind the testis into the gelatinous tissue (Figure 3, *lig. g. g.*) that is fused with the gelatinous tissue of the dorsal surface of the mantle. However, the ligament is recognizable externally and then descends with the tissue of the end of the body into the cone, filling its cavity, which is at first open and later closed, but without reaching the tip.

The **seminal vesicle** and the end of Needham's pocket of the male are situated on the anterior half
229 of the caecum and on the dorsal side of the left branchial heart. The efferent duct is visible behind the base of the left gill and is spatulate, as in *Chiroteuthis.*

There is no trace of hectocotylization and no distinct grouping of suckers on the ventral arms.

Measurements

Dorsal length of mantle (length of gladius)			83 mm
Ventral length of mantle			80 mm
Length of body to base of ventral arms			109 mm
Total length (including ventral arms)			169 mm
Maximal width of mantle			27 mm
Dorsal length of fins (including tip of body)			62 mm
Maximal width of both fins			60 mm
Width of head			28 mm
Length of left 1st arm			36 mm
Length of left 2nd arm			46 mm
Length of left 3rd arm			38 mm
Length of left 4th arm	60 mm	of right 4th arm	58 mm
Length of club			61 mm

Mastigoteuthis flammea CHUN

Mastigoteuthis flammea CHUN, 1908, p. 88.

(Plate XXXIII, Figures 3, 4; Plate XXXV, Figures 3, 4, 7, 9; Plate XXXVI, Figures 1, 2; Plate XXXVII, Figures 2–4).

Locality: Station 53: Guinea Current, 1°14′ N, 2°10′ W. Vertical net to 3,500 m—One female. Station 64; northern branch of Benguela Current near San Thomé, 0°25′ N, 7°0′ E. Vertical net to 2,000 m—One female.

We caught two specimens with a magnificent dark red coloration in the Guinea Current and the northern branches of the Benguela Current. Both had lost the tentacles, but careful study showed that they belong to a distinct new species of *Mastigoteuthis*.

The specimens have a gelatinous body and the fins are about half as long as the mantle. The head is not widened and the eyes are relatively small; the ventral arms are extremely long.

The **mantle** forms a slender goblet. It tapers posteriorly into a point toward which the posterior margin of the fins slightly extends. The ventral and dorsal corners of the mantle project only little. The dorsal length of the mantle, including the posterior end, is 27 mm in one specimen, 35 mm in the other.

230 The fins are not as large as in *M. cordiformis*, but are about half as long as the mantle. They are slightly longer than wide, rhomboidal in the larger and elliptical in the smaller specimen. The fins continue in narrow membranes at the posterior end of the body, which projects slightly beyond them.

The moderately large **funnel** is situated in a shallow groove, bordered by gelatinous swellings of the head. The funnel cartilage is oblong-oval in one specimen (Plate XXXV, Figure 3), blunt-triangular in the other (Figure 4). It has a tragus and an antitragus; the antitragus is more distinct in the smaller specimen. The opposite mantle cartilage is nose-shaped, with a distinct groove for the tragus and a less distinct groove for the antitragus.

The long **neck cartilage** (Figure 7) bears two longitudinal median ridges and 3 grooves between the ridges and the margin.

The **head** is nearly cylindrical; it has projecting gelatinous cheeks on each side of the funnel. Because of the small eyes, the head is not rounded as in other species of *Mastigoteuthis*. The eye is 3.8 mm wide in the large specimen; in the smaller one it is only 2.2 mm wide.

The **olfactory tubercle** is situated on the cheeklike swellings of the head near the funnel. It has a short stalk and a rounded knob at the end. In the juvenile specimen, the stalk continued into a small gelatinous process that projects like a horn above the knob which is covered with sensory epithelium.

The **arm apparatus** is characterized by the large ventral arms. The other arms are much shorter and differ only little in size. The 2nd arms are the longest, the 1st arms the shortest. All arms are intensely colored on the outer side, which is separated by a sharp edge from the lateral and inner surface. Swimming membranes are present only on the 4th arms, extending broadly toward the dorsal side. The suckers form 2 rows; they are hardly more loosely arranged on the ventral arms than on the other arms. All suckers are surrounded by strongly developed protective membranes; the larger specimen showed an anomaly in the form of an unusually large sucker near the base of the right 3rd arm (Plate XXXV, Figure 9).

The suckers on the arms are nearly spherical and their short stalks are situated on conical gelatinous pads. There are only 3–5 denticles on the dorsal side of the opening. The larger suckers are 0.4 mm wide and the denticles are partly covered by the very thick chitinous ring which lines the inner surface of the sucker.

The **coloration** of the live animal was quite conspicuous: a magnificent dark red on the whole body and the outer side of the arms. It is caused by numerous chromatophores of various tones of red, and by pigment in branched cells of the cutis. The inner side of the arms bears only sparse chromato-
231 phores and was almost colorless in the live animal. The coloration disappeared almost completely after preservation, so that only a few scattered chromatophores, some of them in a single row on the dorsal side, remained recognizable. This coloration is apparently caused mainly by the pigment in the connective tissue of the cutis and less by the chromatophores. The ventral side of mantle and head, the dorsal side of the fins, and the outer surface of the ventral arms bear widely separated, dark pink dots which are surrounded by a reddish stripe (Plate XXXVII, Figure 4). These are luminous organs; they will be described below.

Inner Organization

(Plate XXXVI, Figures 1, 2)

Opening of the mantle cavity shows the delicate, transparent abdominal wall which is exposed almost completely because the septum which connects it with the mantle is situated close to the posterior end of the body. The straight margin of the funnel passes above the rectum and has to be pulled anteriorly as in Figure 1, to show the anus. The band-like funnel depressor extends broadly into the dorsolateral wall of the funnel. It tapers where it extends obliquely along the liver and toward the base of the gills. After removal of the gills, however, the muscle can be followed as a fine fibrous cord posteriorly to the apex of the stomach. A few thinner fibers extend from this muscle toward the base of the gills. Between the insertions of the depressor is the large liver, the posterior end of which projects beyond the base of the gills. The rectum, which is situated on the liver, opens between the large anal lips which bear relatively short lateral appendages. The vena cava passes almost in a straight line to the right of the rectum and close by it before descending into the renal sac. The whole abdominal wall from the anus to the anterior part of the renal sac was reddish in the larger specimen. The renal papillae (*ur.*) project in the form of a chimney; the long, funnel-shaped inner openings of the renal sac behind them are visible after opening of the renal sac.

The complex of venous appendages (*sacc. v.*) is longer than wide; it consists of 3 parts: one anterior median and two posterior lateral ones. On the posterior margin of the latter parts there are the spherical branchial hearts (Figure 2, *c. branch.*), whose small, spherical appendages (*app. c.*) are visible through the abdominal wall. The base of the gills and branchial heart are widely separated as is characteristic for all representatives of *Mastigoteuthis.* The branchial artery (*a. branch.*) thus forms an extremely long curve between its spindle-shaped dilatation—coinciding with its exit from the branchial heart—and the point where it enters the base of the gill; from there it can be followed for some distance along the inner margin of the branchial gland. The slightly sickle-shaped **gills** are 3 mm long. They consist of 11 lamellae in the larger specimen. A large, delicate ligament (*susp.*) connects the margin of the branchial gland with the inner side of the mantle. The branchial vein passes on the ventral crest of the
232 gill (*v. branch.*), crosses the long branchial arteries near the base and widens into thin-walled atria. They open into the oval heart, which is characterized in this species by the unusual anterior position of the root of the posterior aorta (*a. post.*) and by the onionlike swelling at the base of the posterior and the cephalic aorta.

The abdominal veins (*v. abd.*) extend from the posterior part of the body and open into the venous appendages near the branchial hearts. The mantle veins (*v. pall.*) have a similar course, receiving on one side the splenic veins and a thick branch which extends along the pallial nerve.

Removal of the renal sac and venous appendages shows the large pancreatic appendages (Figure 1, *pancr.*) which accompany the bile duct. They form about 3 lobes, the anterior of which is the largest, especially in the smaller specimen. The lobes extend in a more or less sickle-shaped arrangement ventrally around the exit of the mid-intestine and open together into the **caecum** (*stom. coec.*), which is almost as long as the stomach. The caecum of the larger specimen (Figure 1) was strongly expanded, that of the smaller animal (Figure 2) slightly contracted but still distinctly divided into an anterior part with dense spiral folds (*rad.*), and a posterior blind sac. The **stomach** (*st.*), which is broadly connected with the caecum (Figure 2), too consists of two parts—the anterior (*st.*) having thick muscular walls, while the posterior part is attached to it like a blind sac. In the smaller specimen, the posterior part of the stomach extends almost at a right angle from the anterior part in the dorsal direction. The gastrogenital ligament (*lig. g. g.*), which extends from the stomach, is very long in the younger specimen and widens posteriorly, becomes gelatinous, and then passes into the dorsal gelatinous tissue of the mantle. The **ovary** adheres to this ligament throughout its entire length, as in *M. cordiformis*, and, again like the latter, is separated from the stomach. The ovary of the smaller specimen is only 2.5 mm long and has an only slightly swollen anterior end; that of the larger specimen is almost club-shaped (*ov.*) and fills nearly the whole space between stomach and caecum.

Only closer examination showed that both specimens are females. The oviducts are only little developed, those of the smaller specimen barely 1 mm long and completely covered behind the branchial hearts, or more exactly, behind the spindle-shaped branchial artery. The oviducts of the larger specimen extend dorsal to the branchial heart, obliquely ventrally toward the anterior part of stomach and caecum.

The nidamental glands appear to be absent at first glance, because of the early state of development of the genitalia. However, closer examination shows a number of fine whitish stripes (*nid.*) on the renal sac along the abdominal veins, extending to near the outer openings of the renal sac (*ur.*). These are certainly the "anlagen" of the nidamental gland, which are situated here at exactly the same point as in the Cranchiidae.

233 **Measurements**

	Station 53		Station 64
Dorsal length of mantle	27 mm		35 mm
Dorsal base of fin	13 mm		21 mm
Width of both fins	18 mm		
Width of mantle	7 mm		
Length of head from dorsal	5 mm		
corner of mantle to base of arms	5 mm		8 mm
Width of head	5.5 mm		8 mm
Length of 1st arm	7 mm	left arm	14 mm
		right arm	10.5 mm
Length of 2nd arm	12 mm		15 mm
Length of 3rd arm	10.5 mm		11 mm
Length of 4th arm	45 mm		40 mm

Mastigoteuthis glaukopis Chun

Mastigoteuthis glaukopis Chun, 1908, p. 88.

(Plate XXXIII, Figures 1, 2; Plate XXXV, Figures 2, 15, 16; Plate XXXVII, Figure 1)

Locality: Station 261: Indian North Equatorial Current, 4°63′ N, 48°37′ E. Trawl 1,213 m—One specimen.

A well-preserved specimen of a medium-sized species of *Mastigoteuthis* was collected near the East African coast; it is of special interest because it has an intact right tentacle. This species differs from the other species of *Mastigoteuthis* in the vivid reddish-brown coloration and the large eyes. The body is gelatinous, slender, with large ventral arms. Luminous organs are absent on mantle and head, except for two organs on the sinus of the eye. The club of the tentacle occupies two thirds of the length of the tentacle.

The **mantle** is slender, goblet-shaped, with a pointed, gelatinous posterior end. Dorsal length of mantle measures 37 mm, maximal width only 8 mm. The relatively large fins are about half as long as the mantle. Their outline is nearly rhomboidal, with rounded corners. The posterior end of the body projects beyond the fins but is surrounded by fine membranes extending from the fins. The dorsal and ventral corners of the mantle project only slightly.

234 The **funnel** is of medium size; the adductors, two on each side, show whitish through the shallow funnel groove. The funnel cartilage (Plate XXXV, Figure 2) has only a tragus but no antitragus; however, the thin lamella of the cartilaginous groove is slightly inflated at the position of the antitragus, so that it gives an indication of an antitragus. The opposite cartilage of the mantle is nose-shaped and shows a distinct depression for the tragus.

The **head** is of medium size and is almost completely occupied by the relatively large eyes. They are spherical, 5.5 mm wide, i.e. twice as large as those of a specimen of *M. flammea* of about the same size. The lid margin of the right eye has a large sinus; there is a shallow sinus on the left eye in which the lid was strongly expanded. Behind the eye and anterior to the funnel one sees the olfactory tubercle, which has a short stalk and is situated on an obliquely directed gelatinous pad of the neck.

The **arm apparatus** shows the typical characters of the genus *Mastigoteuthis*; the ventral arms are much longer than the other arms. Arm formula: 4, 2, 3, 1. Swimming membranes are barely indicated on the 1st, 2nd and 3rd arms; those of the 4th arms are well developed and situated on the dorsal side, but they are not as wide as in the other species. All arms have a pigmented outer surface which is separated by an edge from the light-colored lateral surface. Protective membranes are well developed everywhere.

The suckers have conical denticles around the opening; the denticles are slightly larger on the dorsal than on the ventral side. The apex of the denticles is sometimes rounded, so that the margin of the sucker appears indented. There are 5–7 larger denticles on the dorsal margin, their number depending on the size of the sucker.

The whiplike **tentacle** (Plate XXXV, Figures 15, 16) is 84 mm long, the club 58 mm. The club thus occupies more than two thirds of the length of the tentacle but it is not widened or distinctly differentiated from the stalk. The club has no swimming membrane and only indistinctly undulate protective membranes. The club begins proximally with very small, scattered suckers and then widens so that it occupies one half of the surface of the tentacle. The suckers extend distally also to the outer side, and leave only about one third of the periphery free; the suckers are situated so close together at one point that their margins touch.

The suckers of the tentacle become slightly larger distally; only the tip bears again smaller suckers. They form oblique rows and are about 0.1 mm wide. Because of the small size of the suckers, the denticles at the opening are difficult to distinguish from the small conical tubercles around them. There are 10–12 small denticles at more or less regular intervals around the opening.

The **buccal membrane** has 7 points and is chocolate brown on the inner side. The attachments are very delicate and typical for the Chiroteuthidae, i.e. the 4th arms are attached ventrally. The buccal cone is high and has laterally a narrow outer lip which appears as a whitish margin surrounding the fluted inner lip whose grooves end in villi.

Coloration. The basic shade of the body and outer side of the arms is a very vivid rust-red; the color is
235 caused by the numerous chromatophores and the pigmented connective tissue of the cutis. Only sparse chromatophores are present on the inner surface of the arms and on the tentacles; on the club they are present only in the area lacking suckers.

I could not find the peculiar luminous organs which are situated on the mantle of some species of *Mastigoteuthis*. However, this species has two luminous organs, one on the ventral margin of the sinus of each eye. These organs are about 1 mm wide and are whitish, in contrast to the rust-red lid margin in which they are embedded. A detailed description of these organs will be given together with that of the other luminous organs of *Mastigoteuthis*.

Mantle Complex

The mantle complex of this species closely resembles that of *M. flammea*. This applies particularly to the form and relative size of the stomach and caecum, which are almost of equal length and are divided into an anterior and a posterior part. As in other species of *Mastigoteuthis*, the gland is situated entirely on the gastrogenital ligament. The ovary is only 1.5 mm long.

The only distinct difference from *M. flammea* concerns the posterior aorta, which originates in the posterior part of the heart. This aberrant condition in *M. flammea* is apparently caused by secondary rotation of the heart in the axis of the atria.

The gills are slender, pyramidal, 6 mm long. They extend to the mantle cartilage and have 21 lamellae on the outer surface.

Luminous Organs
(Plate XXXVII)

Verrill (p. 298) noted in his description of the large *M. agassizii* that the body is uniformly covered with ring-shaped, light-brown spots which surround a purplish brown central spot. These are characteristic cutaneous organs, as was proved by Joubin (1893, 1895), who described them in detail for *M. grimaldii*. Joubin considers them as an "oeil thermoscopique", i.e. a very sensitive thermometer which perceives the temperature of the environment. This interpretation has found its way into textbooks, e.g. Lang's Comparative Anatomy. Before entering the discussion whether there is no other interpretation of their function, they are described again.

236 I can confirm Joubin's description of their relatively simple structure, at least in *M. flammea*, which also has such organs.

The luminous organs of *M. flammea* are scattered on the mantle, more densely on the ventral than on the dorsal side. The fins, however, bear organs only on their dorsal surface. There are also organs on the ventral surface of the head and on the ventral arms. Preservation destroys the red coloration,

except for the luminous organs which remain distinctly visible as blackish red dots. Each organ is surrounded by a thin circle, which in turn is surrounded by dark pink pigment (Plate XXXVII, Figure 4).

Sections of these organs (Figures 2, 3) show that they are embedded in the gelatinous connective tissue of the cutis and are not situated as close to the surface as described by Joubin for his species. Each organ contains a cup which consists of loosely arranged, finely granulate cells (*phot.*). I never found their outlines to be as sharp as those illustrated by Joubin, nor did I detect a regular arrangement of cells in a single layer, resembling an epithelium, as he described. The outline of the cells is only distinct at points where there are gaps between them. Their protoplasm is finely granulate; however, it shows radial striation directed toward the center of the cell at some points. The nuclei stain intensively and are usually spherical, but some of them have an irregular form. They are uniformly filled with chromatin having larger and smaller granules.

These cells form a cup open toward the surface. However, the cup is not closed inwardly but contains a central or lateral canal; a cord enters this canal and extends toward the lower surface of the chromatophore (see below), where it widens to form of an umbrella. The cord (Figure 3, *x.*) contains numerous nuclei, some of them small and rounded, others oval or irregularly indented. The umbrella-like widening contains larger, often irregularly formed nuclei, usually in groups of 2 or 3. Joubin described this structure in detail and considered it to be a nerve to the chromatophore. I was at first inclined to accept this, but later entertained doubts because of the marked difference between this structure and that of typical nerves. Nerves always have elongate nuclei and a more distinct fibrillar striation. I also failed to find a thicker nerve outside the organ, from which this cord could originate. I tend, therefore, to interpret the whole structure as connective tissue, forming supporting apparatus for the chromatophore, but cannot give more definite information on this peculiar formation.

Gelatinous connective tissue fills the space between the axial formation and the inner wall of the cup.

237 Joubin already noted that the most conspicuous structure is a large chromatophore that closes the cup to the outside. It contains, in addition to its muscular processes, a large central nucleus (Figure 3, *chr.*). The pigment is blackish pink. Joubin (p. 43) described some differences between this chromatophore and others, e.g. the swollen form, the short, numerous fibers which extend from it, the assumed ending of the nerve, and the abundant pigment. These differences from other chromatophores are valid also for our species, but they are certainly still true chromatophores and resemble e.g. some of the superficial chromatophores of *Chiroteuthis.*

The whole organ is surrounded by a loose envelope of pigment in the form of branched cells of connective tissue or pigmented meshes of the glatinous tissue, which are dark pink. They cause the diffuse pigmentation in the more distant vicinity of the chromatophore. Joubin also described blood vessels (*v.*) which branch in the vicinity of the organ.

Joubin assumes that the large chromatophore absorbs light from the outside but passes heat rays, so that the chromatophore forms a dark lens-shaped screen: "un cristallin noir d'un oeil chargé de percevoir les rayons obscurs; c'est un oeil thermoscopique." He considers accordingly the cup of large light cells as supporting cells, or perhaps as a mirror which reflects the heat rays toward the nerve.

Joubin realized the difficulties of this interpretation. Without entering into a detailed discussion, I shall only stress that it would be very striking indeed if *Mastigoteuthis* possessed a thermal apparatus which is absent in all other Cephalopoda and, moreover, in all the pelagic deep-sea forms. It would be difficult to explain why a sensitive deep-sea thermometer should be present precisely in these forms and absent in the other deep-sea forms. In my opinion it would be more natural to consider these structures as luminous organs. The cup of large cells, with its spherical nuclei, represents the luminous

body in front of which is situated a color filter, i.e. the chromatophore. The chromatophore of preserved specimens is always contracted, so that part of the light emitted by the luminous body could pass the margin of the chromatophore in the light-colored zone described above. If, however, the chromatophore is extended, the light could still pass, but it would receive a certain color. In any case, this interpretation needs confirmation by observation of the live animal, which would make it possible to decide whether these are phosphorescent organs.

The assumption that these "thermoscopic eyes" are luminous organs was strengthened considerably by the fact that *M. glaukopis* has organs which consist mainly of a luminous body but lack a chromatophore situated in front of it. As stressed in the systematic review (p. 176), this species has no cutaneous
238 organs like those described above, but the ventral margin of the sinus of each eye bears a whitish shining organ which is 1 mm long (Figure 1). This organ consists mainly of a large luminous body (*phot.*), formed by those finely granulate cells with spherical nuclei which we have already seen elsewhere. The cells are also loosely arranged, with intercellular spaces which contain numerous capillaries with elongate nuclei. The capillaries extend from thicker vessels on the inner margin of the organ (*v.*). The whole organ is embedded in the cutis which consists of gelatinous tissue (*gel.*). Numerous muscular fibers (*mu.*) extend on the outer surface toward the margin of the lid fold. The organ is again surrounded by diffuse pigment which is denser at the outer surface. There is a ring of pigment toward the inside at a greater distance from the organ. A lens or reflector is not recognizable. Nerves are certainly present, but I could not find them.

2. Subfamily: *Chiroteuthinae*

Chiroteuthis D'ORBIGNY, 1839

Loligopsis veranii FÉRUSSAC, *Mag. de Zool.*, Classe V, Plate 65, Figures 1–10.
Chiroteuthis veranyi D'ORBIGNY, 1839, *Ceph. acét.*, p. 325, "Calmaret"; Plate II, Figures 1–10; Plate IV, Figures 17–23.
Loligopsis verani VÉRANY, 1840, *Céph. médit. présentés Congr. Turin*, Figure 19.
Loligopsis meridionalis RISSO, 1843, *Catal. Céph. comm. Congr. Lucca* (observ. de Vérany, Congr. Milan, 1844, p. 7).
Loligopsis veranyi VÉRANY, 1851, *Ceph. Médit.*, p. 120, Plates XXXVIII, XXXIX.
Chiroteuthis bonplandii? VERILL, 1881, *"Blake" Rep. Mus. Comp. Zool.*, p. 102, Plate III, Figure 1; *N. Am. Ceph.*, Plate XLVII, Figure 1.
Chiroteuthis lacertosa VERRILL, 1881, *N. Am. Ceph.*, Plate LVI, Figure 1.
Chiroteuthis (?) sp. HOYLE, 1886, *Rep. Chall.*, p. 178, Plate XXXI, Figures 1–5.
Chiroteuthis veranyi WEISS, 1889, *Org. C. fish.*, p. 77, Plate VIII, Figures 4–8
Chiroteuthis veranyi JOUBIN, 1893, *Org. colorés Chirot.*, p. 331, Figures 1–12.
Chiroteuthis picteti JOUBIN, 1894, *Céph. Amboine*, p. 40, Plates I, II.
Cheiroteuthis macrosoma GOODRICH, 1896, *Ceph. Calcutta "Investigator"*, p. 12, Plate III, Figures 51–57.
Cheiroteuthis pellucida GOODRICH, 1896, *ibid.*, p. 14, Plate IV, Figures 58–61.
Chiroteuthis veranyi FICALBI, 1899, *Chirot. et Doratopsis*, p. 106, Plate I, Figures 4, 7, 10, 13–15.
Chiroteuthis veranyi JOUBIN, 1900, *Camp. Scient. Monaco*, p. 88.
Chiroteuthis veranyi, picteti, macrosoma, pellucida PFEFFER, 1900, *Syn. Oeg.*, pp. 184–186.
Chiroteuthis veranyi CHUN, 1903, *Leuchtorg.*, p. 74, Figure 3.
Chiroteuthis macrosoma NISHIKAWA, 1906, *Rare Ceph. Dob. z. Tokyo*, p. 109, Plate.
Chiroteuthis imperator CHUN, 1908, *Ceph. Deut. Tiefsee-Exp.*, p. 88.
Chiroteuthis imperator, macrosoma, veranyi HOYLE, 1909, *Cat. Ceph.*, II, p. 274.

This is one of the most splendid deep-sea Cephalopoda. It was discovered by VÉRANY, who found

a specimen with large arms and large, whiplike tentacles on the surface of the sea near Nice on 14 April
239 1834. VÉRANY sent his specimen with a description and a drawing to FÉRUSSAC, who was just planning the publication of his comprehensive work on the Cephalopods. FÉRUSSAC reported on VÉRANY's discovery on 27 October 1834 before the Académie des Sciences and described the new species as *Loligopsis veranyi.* The report contained an illustration according to VÉRANY's drawing, which later appeared in the monograph of FÉRUSSAC and D'ORBIGNY. D'ORBIGNY established in this monograph in 1839 the new genus *Chiroteuthis* for this species, which he named *Ch. veranyi* (p. 326), but the old name *Loligopsis veranyi* is retained on the plate. The latter name was also used by VÉRANY (1851), who objected to the consonance of the names *Chiroteuthis* and *Cirroteuthis.*

A torn-off tentacle of *Ch. veranyi* was described by VERRILL (1881) from the *Blake* material from the Caribbean Sea (lat. 41°34'; long. 65°54'). *Ch. veranyi* occurs also in the open sea, which was proved by the capture of numerous specimens at different depths along the east coast of the U.S.A. These specimens were described by VERRILL (1881, p. 408) as *Ch. lacertosa.* However, PFEFFER stated that they are identical with *Ch. veranyi.*

The presence of *Chiroteuthis* in the Pacific was established in the *"Challenger" Report*, in which HOYLE (1886, p. 178) described fragments of a gladius from the stomach of a shark. The gladius of the Chiroteuthidae is so characteristic that even fragments can be recognized with certainty. The fragments were definitely those of a gigantic specimen, whose gladius reaches a length of 1 m.

The first information on the soft parts of Indopacific forms was obtained by PICTET and BEDOT, who collected damaged specimens in the Amboina area which were described by JOUBIN (1894) as *Ch. picteti.* The studies of the *Investigator* proved the occurrence of these forms in the Bay of Bengal. A well-preserved specimen, but without tentacle clubs, was described by GOODRICH (1896, p. 12) as *Ch. mascrosoma.* Whether this species is identical with *Ch. picteti* is difficult to decide, because precisely the suckers on the tentacles, which show the distinctive characters, are absent.

A well-preserved specimen caught by the Deep-Sea Expedition at Station 190 south of Sumatra (Plate XXXVIII) resembles the above species in characteristic form. This is the largest known specimen of *Chiroteuthis* of which the soft parts are preserved. I obtained similar specimens from the Sagami Bay, Japan, which were collected by HABERER and DOFLEIN. They are apparently quite common there, as I have young and old specimens of different stages—some of them well preserved. It seems that they are identical with the specimen described by NISHIKAWA as *Ch. macrosoma* GOODR.

I thought at first that the species found near Sumatra and near the coast of Japan is identical with *Ch. picteti* and *Ch. macrosoma.* However, comparison with JOUBIN's types from the Geneva
240 Museum convinced me that there are differences in the form of the suckers of the tentacles. I shall therefore describe the new species as *Ch. imperator.* Further study will show whether this name is valid; the clubs of *Ch. macrosoma* are unknown and it is therefore not certain whether *Ch. macrosoma* belongs to the group of *Ch. picteti* or to that of *Ch. imperator.* However, it is certain that there is a group of Indopacific forms which differs from the Atlantic–Mediterranean form in its characteristic form and also in the form of the posterior part of the body, the luminous organs on the eyes and the suckers of the club. The Indopacific group could be considered as a subgenus, for which I propose the name *Chirothauma.*

The specimen described by GOODRICH (1896) as *Ch. pellucida* from the Bay of Bengal is apparently a juvenile *Ch. picteti.* The differences between the species of *Chiroteuthis* are given in the following table:

Posterior end of body level with fins. Ventral side of eyes with two luminous stripes and a few isolated organs.	Head rounded. Eyes very large, slightly protruding. Stalks of suckers of tentacles with a pigmented ring. *Ch. veranyi* FÉRUSSAC, 1834.
Posterior end of body projecting in the form of a spindle beyond posterior margin of fins and bordered by an accessory seam. Ventral side of eyes with 3 rows of lens-shaped luminous organs.	Head cylindrical. Stalks of suckers of tentacles smooth. Denticles of suckers of tentacles with a spherical basal swelling. Suckers of arms with crenelated denticles dorsally. *Ch. picteti* JOUBIN, 1894. Head spindle-shaped. *Ch. macrosoma* GOODRICH, 1896. Head cylindrical. Eyes not protruding. Stalk of suckers of tentacles with an unilateral wing-shaped widening. Suckers of arms with crenelated denticles dorsally. *Ch. imperator* nov. sp.
Posterior end of body projecting beyond fins in the form of a spear; without seam.	Stalk of suckers of tentacles smooth. Suckers of arms indented ventrally with large denticles dorsally. *Ch. pellucida* GOODRICH, 1896. (Juvenile form of *Ch. picteti?*)

241 ## Subgenus *Chirothauma*

Chiroteuthis (Chirothauma) imperator n. sp.

(Plate XXXVIII, Plate XXXIX. Figures 1–10; Plate XL, Figures 2–5, 7; Plate XLI; Plate XLII, Figures 1–4; Plate XLIII; Plate XLIV, Figures 3, 6–16)

Locality: Station 194: Nias South Canal, 0°15′ N, 98°8′ E. Trawl 614 m.

The gelatinous body is slender; the fins are long and together form a nearly circular disk. The spindle-shaped posterior end of the body projects markedly beyond the posterior margin of the fins and is bordered by narrow delicate membranes which are not fused with the fin situated anteriorly to them.

The head is very long and cylindrical. The eyes do not protrude and bear 3 rows of luminous organs on the ventral surface.

The arm apparatus is strong and characterized by powerful ventral arms and long, whip-like tentacles. The suckers of the long club have wing-shaped widenings on the stalk.

This beautiful, large species from Nias near the west coast of Sumatra is apparently widely distributed in the Indopacific region; I have several specimens, collected by HABERER and DOFLEIN in Sagami Bay, Japan. The large gladius found by the *Challenger* Expedition in the stomach of a shark in the Pacific possibly belongs to this species. HOYLE correctly considered this gladius as belonging to the genus *Chiroteuthis*.

The species described by GOODRICH as *Ch. macrosoma* from the Bay of Bengal may be

identical with *Ch. imperator*, but this cannot be decided, because an important character of *Ch. imperator*—the wings on the stalk of the tentacle suckers—cannot be checked on Goodrich's specimen, as its clubs are lost. That *Ch. imperator* and *Ch. picteti* should be identical seems to me to be at least doubtful: the absence of wings on the stalk of the tentacle suckers, and the different dentition of the arm suckers are too distinct to consider these two forms as identical. Should it, however, transpire that these characters are not constant, then all the species which I designated *Chirothauma* would have to be placed in the single species *Ch. picteti* Joubin. The following description is based mainly on the specimen caught by our expedition; it is the largest specimen known. The specimens from Sagami Bay were particularly valuable; only one of them was slightly smaller, the others were juvenile specimens.

The **mantle** is long, goblet-shaped; it ends posteriorly in the gelatinous end of the body. The body projects beyond the posterior margin of the fins; it has the form of a spindle and the tip has the form
242 of an arrowhead. The dorsal corner of the mantle projects markedly, the ventral corners are not recognizable. The specimen from Station 194 has a dorsal mantle length of 209 mm; the posterior point of the body was broken off.

The **fins** are large, strongly developed, 100 mm long and 90 mm wide. Except at the anterior part of the base, they are fused dorsally into a nearly circular disc the posterior margin of which does not show a heart-shaped indentation. The spindle-shaped posterior end of the body projects at least 30 mm beyond the fins and has delicate lateral membranes which are about 3 mm wide and project a short distance ventrally beyond the fins; the membranes are not fused with the posterior margin of the fins. These membranes lack the characteristic musculature of the fins and therefore cannot be used for movement.

The **mantle cartilage** (Plate XXXIX, Figure 10) is nose-shaped and its apex is situated between the tragus and antitragus of the funnel cartilage. It bears corresponding grooves for the 2 processes, of which that for the tragus is more distinct. The mantle cartilage is 9 mm long from the mantle margin.

The long, narrow **neck cartilage** (Plate XXXIX, Figure 1; Plate XLIII, Figure 3) is 32 mm long; it is 5 mm wide anteriorly, 4 mm posteriorly. It has a shallow median groove along its whole length, which corresponds to the low ridge of the opposite cartilage. This has a cartilaginous margin which surrounds the neck cartilage completely. The opposite cartilage of the neck is 6 mm wide.

The **funnel** is moderately developed, 31 mm long. Its opening is relatively small, curved ventrally and contains a valve in all specimens, including the juveniles. The adductors are not visible externally but shine through whitish in preserved specimens. They form two long muscles (Figure 24) which extend on the ventral side posteriorly from the posterior margin of the cranium and divide on each side into two branches which Brock (1880, p. 15) named "musculus adductor superior" and "inferior" in *Onychoteuthis*. The terms "anterior" and "posterior" are more suitable. The posterior muscle is always thicker than the anterior one. The funnel is fused laterally and dorsally with the musculus collaris, which extends toward the posterior lateral surface of the neck cartilage. Both funnel cartilages (Plate XXXIX, Figures 8, 9) are situated on the slightly projecting sides of the funnel. They are nearly oval
243 and 6 mm long. Their flat lateral margin projects slightly from the surface and is broadest posteriorly near the respiratory cavity. The margin of the right cartilage (Figure 9) was slightly folded over, that of the left cartilage (Figure 8) flat. As in most Chiroteuthidae, the funnel cartilage of *Ch. imperator* has a lateral tragus and a posterior antitragus. The tragus is situated on the ventral lateral margin and is slightly longer than the antitragus.

According to Joubin (p. 45, Plate II, Figure 15), the antitragus of *Ch. picteti* consists of two fused tubercles. Examination of his specimens showed, however, that the antitragus always consists of a single cartilage. This is shown in Figure 25, based on an original specimen of Joubin.

The **funnel organ** (Plate XLII, Figure 1) is well developed. Its single dorsal part (*org. inf.*[1]) is

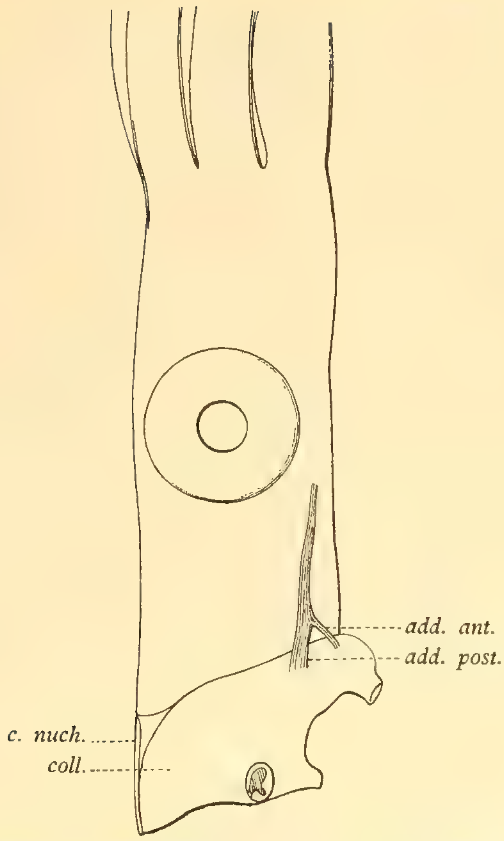


FIGURE 24. *Chiroteuthis imperator.* Funnel adductors: *add. ant.* anterior adductor; *add. post.* posterior adductor; *c. nuch.* neck cartilage; *coll.* collaris.

FIGURE 25. Funnel cartilage of *Chiroteuthis picteti* JOUB.

heart-shaped with the apex anteriorly. The paired central parts (*org. inf.*[2]) are oval.

The **head** is unusually long; it is 63 mm long from the dorsal mantle corner to the base of the arms, 69 mm from the ventral mantle margin. It is cylindrical, without protruding eyes, at least in large specimens. This is in contrast to the head of *Ch. veranyi,* in which the large eyes cause the rounded form of the head (Plate XL, Figure 1).

The **neck,** which extends from the anterior margin of the collaris and funnel to the lower margin of the eye, bears no folds. Except for the funnel adductors, there are no distinct muscles in this region.

The arm musculature extends into a continuous cephalic and cervical muscular tube which is covered by the cutis with a honeycomblike pattern. It contains longitudinal muscles from the base of the arms to the upper and lower margin of the orbit.

The **eyes** (Plate XLIII, Figures 2, 4) are situated in the middle of the head and do not protrude, giving the head part a cylindrical shape. Their contour is almost circular and they are flattened in the main axis. The eyes of our specimen are 23 mm in transverse diameter and their main axis measures about 15 mm. Only a narrow median bridge separates the eyes, since the head is about 32 mm wide. The eyes are thus quite large. However, they are relatively smaller than the impressive eyes of *Ch. veranyi,* which are almost as large as the visceral sac. The eyeball is blackish grey; the iris is 6 mm wide and has a metallic sheen. The slightly convex lens covers the pupil, which is 9 mm wide.

The blunt-triangular optic ganglion is situated on the posterior inner side of the eyeball, slightly
244 closer to the dorsal side (Plate XLIII, Figure 4, *g. opt.*). It is flattened in the main axis of the eye and

its maximal width is 13 mm. The irregularly lobed white body (*c. alb.*), which adheres closely to the eyeball, surrounds the ganglion.

An extraordinary feature of the eyeballs are the three rows of luminous organs, gleaming like a necklace of precious stones. They are situated on the ventral side of the eyeball (Plate XLIII, Figure 2). They are also present in *Ch. picteti*, but they were overlooked by Joubin. Figure 6 of Plate XL shows the organs of *Ch. picteti* after the original specimen. *Ch. veranyi* also has luminous organs, which were not known until now. However, they are fused into two ventral stripes (Plate XL, Figure 1), while those of *Ch. imperator* and *Ch. picteti* remain separate.

The form of the lid margin varies in the different specimens according to the state of contraction. If it is moderately contracted, the posterior margin is flattened and the anterior margin semicircular with a more or less distinct sinus. The posterior lid margin, or lower eyelid, is thickened into a crescent. Sections of this margin show a marked thickening of the ring muscle which surrounds the lid margin (Plate XLIII, Figure 2, *mu. palp.*).

The **olfactory tubercles** (Plate XL, Figure 5) are situated on the neck at the level of the lower margin of the eyes, about 8 mm from them. They are 1.5–2 mm long and consist of three parts: a short stalk into which enters the olfactory nerve, as is distinctly visible in the cutis; an acorn-shaped capitulum covered with olfactory epithelium; and an apex, curved like a bird's beak.

Goodrich noted the presence of olfactory tubercles in *Ch. macrosoma*, but Joubin does not mention them in *Ch. picteti*.

Arm Apparatus

The arm apparatus is large, as is the case in all *Chiroteuthis*. Particularly large are the ventral arms and the enormous whiplike tentacles with their long clubs.

The arm formula is 4, 3, 2, 1.

The 1st (dorsal) arms are 100 mm long. They are more or less triangular in cross section and have a flattened inner surface with suckers and a keel (swimming membrane) on the outer surface which is weakly developed and distinct only in the distal part.

The 2nd arms are 126 mm long. Their cross section forms an equilateral triangle with rounded sides. Their swimming membrane is more strongly developed than that of the 1st arms and is slightly displaced ventrally.

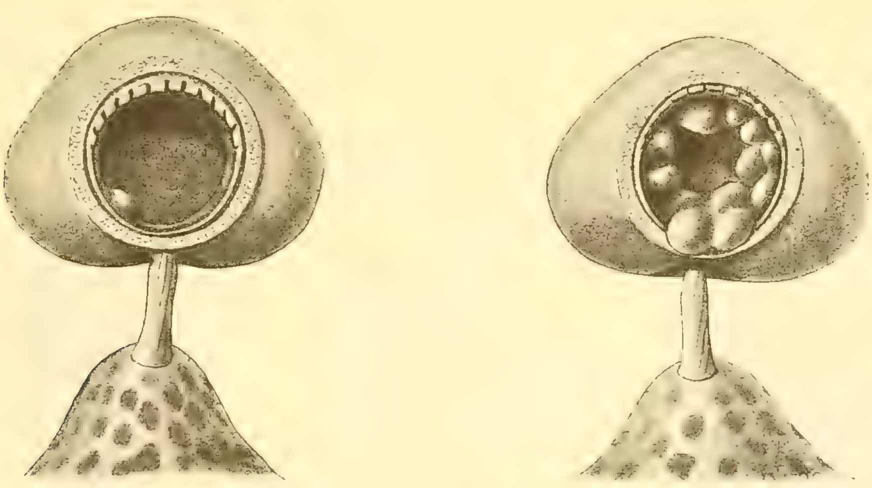
245 The 3rd arms are 156 mm long and have a wide swimming membrane which, too, is displaced slightly ventrally and extends toward the 4th arms at the base, surrounding the tentacles. The protective membranes are distinct.

The 4th arms vary markedly in length. They are 302 mm long in the specimen from Station 194; those of a slightly smaller specimen from Sagami Bay are 218 mm long. A still younger specimen from Sagami Bay (Plate XLI, Figures 10, 11), the gladius of which is 192 mm long, has very long ventral arms: 265 mm. They have a flattened outer surface; their ventral lateral margin forms a sharp edge, while the dorsal margin foms a large swimming membrane which is 12–14 mm wide. The ventral arms have an irregularly square cross section. The protective membranes are distinct and the suckers form a single row at the tip. The suckers are not markedly smaller or more widely spaced than they are on the other arms. A distinctive character of the ventral arms are the luminous organs, which form strongly pigmented, shining bodies near the dorsal protective membrane and alternate more or less with the dorsal row of suckers. The proximal organ is situated close to the base of the tentacles. The luminous organs extend along the

whole arm to the tip, where those that are still developing are densely arranged (Plate XLIII, Figure 4, *luc.*). The specimen from Sumatra has 58 organs on the right arm and 55 on the left arm; the arms of the specimen from Sagami Bay bear 52 organs.

The **suckers of the arms** are arranged in two alternating rows; they become gradually smaller toward the tip. The larger suckers are acorn-shaped and 3 mm wide. They have thin muscular stalks, situated on a pigmented gelatinous cone and inserted in the concave, grooved ventral side of the posterior third of the sucker (Plate XXXIX, Figures 4, 5). The opening of the sucker is surrounded by a dark chitinous ring which is broad dorsally and reaches to the middle of the sucker, but it is very thin on the ventral side. The proximal margin of the ring has a ridge which extends obliquely on the sucker (Figure 4). The dorsal half of the opening bears 10–12 densely arranged crenelated denticles which become larger toward the middle (Figure 5). The chitinous ring is finely granulate near the denticles, especially on the dorsal side.

According to JOUBIN, the suckers of *Ch. picteti* have crenelated denticles on the ventral side and there are additional rounded tubercle-like denticles which are irregularly distributed inside the sucker (p. 51, Plate 2, Figure 7). As PFEFFER (p. 185) stated, this condition is so unusual that I examined the suckers of the type specimens in Geneva. It appeared that many suckers show the normal pattern described above, with 10–12 crenelated denticles on the dorsal margin of the ring (Text Figure 26 a). In other suckers the chitinous ring forms hump-shaped thickenings inside its cavity, sometimes so
246 numerous that they reach the outer margin (Text Figure 26 b). But such suckers, which are apparently pathological, always also have distinct crenelated denticles at the dorsal margin.



a b

FIGURE 26. *Chiroteuthis picteti* JOUB. Suckers of the arms.

The suckers of the arms of *Ch. picteti* are thus not exceptional in their dentition.

The **tentacles** are very long, several times as long as the body; they are longer or shorter according to the state of contraction. Those of one specimen from Sagami Bay are 760 mm long. The tentacles have a circular cross section; they are whiplike, with pigmented glandular knobs on the outer side.

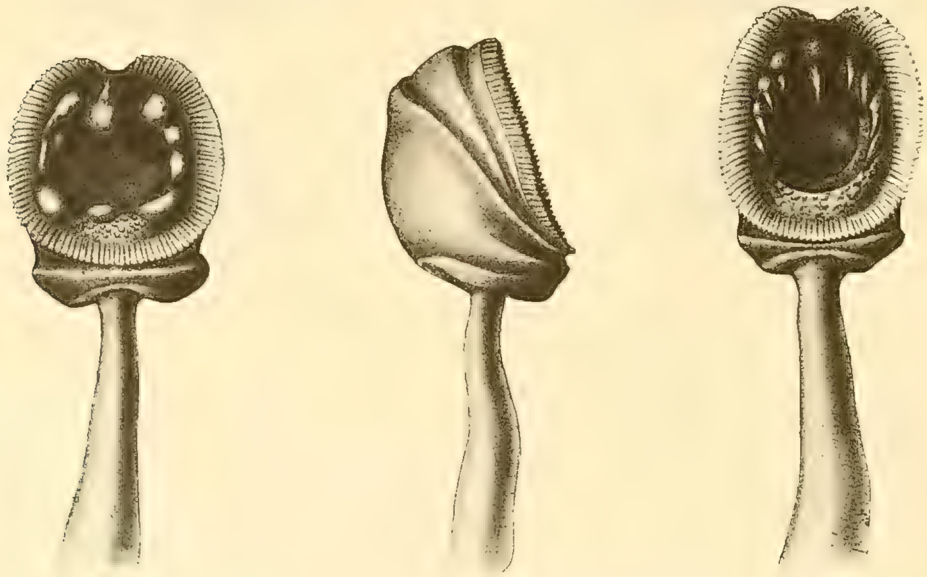
The **club** also varies in length; it is 118 mm long in the specimen from Sumatra and 143 mm in a large specimen from Sagami Bay. The club is sometimes extended, sometimes curved back. A swimming membrane is absent, but the protective membranes are very strong and symmetrical; they narrow proxi-

mally and distally and are 3–4 mm wide in the middle. The membranes are distinctly delimited from the stem on the outer side of the club. The stem is swollen at the end into the form of a spoon or bottle and forms a fingerlike, violet glandular knob which projects beyond the tip of the club. The protective membranes contain thick, triangular, regularly spaced muscular supports which are contiguous at the base and extend obliquely to the stem, with their tips directed distally (Plate XL, Figure 4). These muscular supports consist of fine fibers arranged transverse to the longitudinal direction; Joubin considered them incorrectly as cartilaginous. The membranes often cover the suckers for a long distance on
247 both sides, but sometimes they are curved outward (Plate XXXVIII). These differences are obviously due to the contraction of the muscular supports, of which there are 83 on each side of the longest club.

The **suckers of the tentacles** have long stalks and form 4 longitudinal rows. The stalks of the outer rows are longer (measuring about 3 mm) than those of the median rows. The suckers form the usual oblique rows of 4. Adjacent suckers of the outer and inner rows form pairs and alternate at their base with the muscular supports (Plate XL, Figure 4). This therefore leaves a bare space in the middle of the club which forms a zigzag stripe and is covered with chromatophores. Joubin did not show this condition distinctly enough in his diagrammatic drawing (Plate 2, Figure 6). The stalks and suckers do not bear chromatophores.

The stalks are slender and usually so transparent that the nerve in them is visible. They are wider at the base and the stalks of the outer and median rows bear winglike appendages at midheight. The stalks differ in this respect from those of *Ch. picteti*, in which such wings are absent according to Joubin's drawing and my observations. The dark-pigmented circular swelling which is characteristic for the stalks of *Ch. veranyi* is absent in *Chirothauma*.

The **suckers** (Plate XXXIX, Figures 6, 7) resemble a helmet with closed visor in lateral view. They are higher than wide and contain a chitinous ring which is light-colored in young specimens, dark-brown



a b c

FIGURE 27. *Chiroteuthis picteti*. Suckers of the tentacles.

in older ones and does not cover the muscular pad at the bottom of the opening. The outer opening of the ring is oval or half elliptical. The ring covers the entire dorsal surface but narrows markedly on the ventral side below the opening of the sucker. Here it forms a deep groove which disappears gradually on the lateral walls. The margin is folded over at the opening; it is indented dorsally in the middle and consists of a peripheral circle of thin chitinous rods and of polyhedral chitinous lamellae which surround the opening in 2 or 3 concentric layers.

There are 9 sharp denticles on the dorsal margin, the median being the largest. As the long club bears 332 suckers, all equipped with such denticles and nearly all acting when the club clasps the prey, their value in the capture of prey is obvious.

Joubin described the suckers of the tentacles of *Ch. picteti* differently; he states that there is only a single dorsal denticle, that other denticles are absent, and that there is a sinuate chitinous margin around the opening. Examination showed that Joubin described an extreme condition which is apparently the last stage of a series of probably pathological modifications. Thus, I found several suckers which had, in addition to the median denticle, 8 lateral denticles that were swollen at the base (Text Figure 27 c). Sometimes only these basal swellings are present, with small apical points or without
248 them (a). In one case the swellings are fused into a ring which narrows the opening, while the dorsal denticle has a bizarre, elongate, whiplike form. This again apparently manifests a rare abnormal dentition.

Glandular Knobs of the Tentacles

A special character of *Chiroteuthis*, absent in all other Cephalopoda, are the pigmented knobs on the outer side of the stalk of the tentacle.

Earlier authors considered them as modified suckers, ignoring the fact that even if there are suckers on the stalk, they are never present on the outer side. After a detailed study, I have come to the conclusion that they are glands with a perhaps poisonous secretion. I name them therefore **glandular knobs.** I found 39–49 such knobs on the different tentacles, the largest being oval and 3 mm long. They are embedded in the gelatinous cutis and are only loosely situated on the musculature. A strongly pigmented muscular ring surrounds the knob like a wall, leaving an outer groove which shows a honeycomb pattern under the magnifying lens. Sometimes the oval knobs have their longitudinal margins slightly raised to form a boat.

The terminal knob on the tip of the club (Plate XL, Figures 2, 3) apparently belongs to the same
249 category. It forms a flask-shaped thickening of the club which is intensively violet, the tip of the club projects slightly beyond the knob. On the outer side of the club, i.e. opposite the sucker-bearing surface, there is a usually oblong oval opening which also shows a honeycomb pattern on the inside.

Examination of the **fine structure** of these knoblike formations (Plate XLIV, Figures 10–16) shows that they are only loosely connected with the stalk and not connected by thicker muscular cords. As noted by Joubin, the knob is surrounded by musculature, but this is completely isolated and forms a ringlike pad which is thickest at the base and continues in the ringlike fold (Plate XLIV, Figures 11, 12, *plica.*) around the opening. The basal muscle fibers consist of longitudinal and radial fibers while circular fibrous systems predominate at the outer margin. Subcutaneous connective tissue is situated between the musculature of the tentacles and the musculature which surrounds the knob. It contains numerous chromatophores which form a closed envelope of pigment around the base and lateral walls of the knobs.

Of particular interest is the tissue which fills the center of the knob. Longitudinal or transverse sections of the knobs (Figures 11, 12) show a pattern which was correctly described by Joubin. Numerous lamellae radiate toward the exterior of the knob; they are widened at some points or connected by oblique bridges. The lamellae of *Ch. imperator*—unlike those shown by Joubin for *Ch. veranyi*—do not project beyond the ring which surrounds the opening; they reveal instead a pattern as shown in Joubin's Figure 6 for *Ch. picteti*. Surface (horizontal) sections of the knob show a completely different picture. There is a delicate, rather regular network (Figure 10) of intensively staining meshes which surround lighter spaces. The meshes vary in size; they are widened in some places, often at the crosspoints. Comparison of the longitudinal and transverse sections shows that the light-colored spaces are cavities which open to the outside.

This tissue is so peculiar at first glance, especially in horizontal sections through the middle of the network, that one can understand that Joubin considered it as a contractile protoplasmic network which protrudes occasionally beyond the margin of the knob to entangle small pelagic organisms.

Detailed study of this extraordinary structure shows, however, that this cannot be correct. As Joubin states, there is an epithelium at the base of the lamellae which gradually flattens and passes into the epithelium of the body (Plate XLIV, Figure 15). This epithelium consists of cubic or cylindrical polyhedral cells which continue for some distance in the basal part of the network and give the impression that these are glandular cells around the irregular cavities. Joubin did not notice that the
250 same cells are present also on the outer side of the network and cover the free end of the lamellae in some places. Another indication that this is a glandular tissue is the presence of masses of secretion (Figure 13, *secr.*) at the base of the network; the secretion stains intensively and lies either free in the lumina or adheres to the network.

Examination of the middle part shows a different picture (Figure 13). The cell boundaries disappear and the granular protoplasmic content of the cells is replaced by a homogeneous, strongly refractile substance with numerous larger and smaller vacuoles. This is obviously a degeneration of the epithelium which, as shown by the sections, begins at the center and spreads toward the periphery. This is illustrated by the longitudinal and horizontal sections in Figures 13–16. Distinctly delimited epithelial cells with spherical or oval nuclei are still present on the gelatinous, vacuolated central mass (*hom.*) in the basal (Figures 14, 15) and peripheral (Figure 16) part. The nuclei in the area in which the cell boundaries have disappeared (Figure 13) always have a peripheral position and are apparently also in a state of degeneration.

The glandular tissue contains numerous capillaries. Since Joubin did not find the blood supply, it should be noted that there are numerous thicker blood vessels along the base of the knob, below the system of lamellae. Vessels enter the network at some points (Figure 14, *cap.*) and pass through its whole length. Horizontal sections show the cross sections of larger and smaller capillaries (*cap.*) which are always situated in a central position and have elongate nuclei in the walls. The nuclei present in the center of the gelatinous mass are therefore those of blood vessels but not remnants of epithelial cells.

Many organs of pelagic deep-sea Cephalopoda, especially luminous organs, show peculiar structures; the one described above is certainly one of the strangest. The whole tissue gives the impression of a vacuolated gland, but it is hard to explain its function. The central tissue, which has degenerated to a gelatinous mass, could hardly have a secretory function. The basal and terminal polyhedral cells could be secretory, because of the presence of masses of secretion in the cavities. These glandular knobs—as I would interpret them because of their structure—probably secrete poisonous substances which stun the captured animals. The possibility, however, that the knobs are luminous organs, cannot be rejected out of hand, though in that case they are of a type completely different from those of all other Oegopsida.

In any case, these structures are certainly not modified suckers. This is untenable because 10-armed Cephalopoda never have suckers on the outer side of the tentacles. Moreover, the musculature around
251 the glandular network cannot perform suction because the pads do not contain radial fibers which would make suction possible. The arrangement of the musculature only shows that the circular fibers protrude the skin fold above the margin of the knob and possibly press the secretion out.

Everything said with regard to the knobs on the tentacle stalk also applies to the terminal knob on the club. This knob also opens on the outer side of the club, i.e. opposite the sucker-bearing inner surface, and is in fact only an enlarged knob of the tentacle. The longitudinal section (Figure 11) shows that the lamellae extend to the skin fold, where they are radially arranged. The network formed by the lamellae (Figure 10) has the same structure as in the other knobs. The musculature around this large knob is less strongly developed, it, too, has no closer connection with the musculature of the club.

Buccal Funnel, Attachment and Coloration

The buccal membrane is raised high above the jaws and lips and ends in 7 points (Plate XXXIX, Figures 2, 3). It is smooth on the outside and has a wrinkled, violet inner side. There are 7 buccal pillars, each with a thick nerve. The ventral pillars are situated close together, the others are regularly spaced. The attachments from the pillars are arranged as described on p. 15 and the 4th arms are attached ventrally. The transparent membranes of attachment extend for some distance on the basal lateral surface of the arms, but they do not pass into the protective membranes. The tentacles are attached, independently from the buccal membrane and its pillars, by a short, thick muscular cord that extends to the base of the ventral arms. The attachments expand the buccal membrane so widely that it covers the base of the arms like a roof. Six slitlike openings, the pori aquiferi, lead to the cavity between the base of the arms and the lower side of the buccal membrane. The two dorsal slits are situated on the base of the dorsal arms, the two lateral slits on the base of the 2nd and 3rd arms, and the ventral slits are situated on the base of the ventral arms.

The **coloration** is bright. The gelatinous body is somewhat transparent and has a flesh pink shade because of the numerous chromatophores scattered all over the skin. The chromatophores are arranged in two layers, one of them superficial, the other situated more deeply and close to the musculature. The chromatophores below the epithelium are usually smaller and more densely arranged than those in the deep layer.

The dorsal side of mantle, fins and posterior end of the body is slightly more brightly colored than the
252 ventral side. The dorsal side near the gladius is more intensively pigmented in some specimens. The head and the arm region, including the swimming membranes, bear numerous brownish pink chromatophores. The pigmentation is particularly intensive on the basal inner side of the arms and on the inner side of the buccal funnel. The stalk and club of the tentacles are also covered with numerous chromatophores, especially around the glandular knobs. The olfactory tubercles and the suckers, including their stalks, bear no chromatophores.

Luminous Organs

VÉRANY (1851 p. 122) noted that the genus *Chiroteuthis* has peculiar organs which form intensively pigmented silvery spots on the ventral arms near the dorsal row of suckers. These organs were examined in detail by JOUBIN (1893), who named them "vésicules argentées" but did not consider them to be luminous organs. In addition to these organs, *Chiroteuthis* has also two other cate-

gories of luminous organs which have been overlooked so far. The first comprises relatively large organs in the mantle cavity, which are situated on the ink sac. These organs were, however, noted by Vérany, who mentioned and illustrated a blue, heart-shaped spot with two large silvery dots. These structures were later considered by Weiss (1889) to be accessory nidamental glands. There are also eye organs which, too, were noticed by Vérany, who illustrated them as silvery bands on the ventral surface of the eyeball. Vérany refers to them as bluish spots ("une tache bleuâtre vive").

The arrangement of the luminous organs is as follows:

The **ventral organs** (Plate XL, Figure 7; Plate XLII, Figures 1, 3, 5, *luc.*) are situated on the heart-shaped posterior end of the ink sac on both sides of the mid-intestine; Weiss (1889, p. 78, Plate 8, Figures 4, 5 and 7) considered them as accessory nidamental glands. They form distinct rounded or oval disks, which are 4.7 mm long and 4 mm wide. In *Ch. imperator* they have a golden or coppery sheen which is most intensive on the outer side. They are embedded deeply in the ink sac and are bilaterally symmetrical. They are innervated by the visceral nerve and receive arterial vessels from the posterior aorta, and a small vessel carries venous blood to the vena cava.

The **organs on the arms** (Plate XXXVIII; Plate XLIII, Figure 4, *luc.*) form a row near the dorsal suckers of the ventral arms. They alternate regularly with the suckers and become smaller toward the tip. There are 24 and 21 organs on the right ventral arms of two large specimens of *Ch. veranyi.* They are more numerous in *Ch. imperator*, in which the ventral arms bear 52–58 organs. Numerous
253 chromatophores cover the organs toward the outer side of the arm. Since a reflector is also present, the light has to pass through the nearly transparent arm, i.e. ventrally.

The **eye organs** (Plate XL, Figure 1) were illustrated by Vérany as two long, golden stripes. There is also a lens-shaped organ anteriorly and posteriorly near the stripe; a third organ is situated between the two stripes.

Ch. imperator has numerous lens-shaped organs which are arranged in 3 rows on the ventral surface of the eye and which glitter intensely and resemble precious stones on the dark background of the eyeball (Plate XLIII, Figure 2, *luc.*^{1}–*luc.*^{3}). The number of these lens-shaped organs is not constant. In a young specimen with an eye 16 mm wide there were 8 organs in the outer row, 8 in the middle row and 6 in the inner row, i.e. 22 organs; the right eye of the specimen from Sumatra has 9 organs in the outer row, 8 in the middle, and 6 in the inner row, i.e. 23 organs. A larger specimen from Sagami Bay (Plate XLIII, Figure 2) has 29 organs: 11 in the outer, 11 in the middle, and 7 in the inner row. The organs are almost contiguous; only the marginal organs are more widely separated.

Histological Structure of the Luminous Organs
(Plate XLIV, Figures 1–9)

The organs differ in structure, but the substance which emits light is easily recognized.

The **luminous body** (*phot.*) is the only component which has the same structure in the 3 types of organ. It is always situated in the center and at first sight seems to consist of a network of gland ducts. Closer examination, however, reveals a structure comprising a dense network of capillaries between which there are large nuclei of the luminous cells (Figures 3, 7, *nu. phot.*). These cells fill the spaces between the capillaries, without, however, defining distinct cell boundaries. Only scant luminous substance occurs in the background of the organs on the arms (Figure 1), where the capillary network is denser; it is more abundant in the foreground (Figure 1, *phot.*). The nuclei are of varying form: oval, rounded or indented; the chromatin is uniformly distributed and consists of larger and smaller granules, of which the latter are often marginal. The plasma between the capillary network is often vacuolated.

The **vascular complex,** which derives from the ventral organs, comprises a dense capillary network, formed by branches of the anterior artery which extend from the renal sacs to the luminous organs (Plate XL, Figure 7) and do not, as is often the case, pervade the reflector, but penetrate the gelatinous tissue toward the inner side of the luminous body. Venous blood passes from the median margin of the
254 organ through a distinct vein which opens in the vena cava at about the level of the anus. Examination with a magnifying lens reveals a fine vasculary network, comprising small, furcating branches in the gelatinous body of the ventral organs.

The conditions in the organs on the arms are similar. The vessels enter laterally and partly centrally, pass the gelatinous body and arrive at the background of the organ, where they divide into the capillary network. The reflector of the eye organs, on the other hand, is often pervaded by thick vessels which then branch into capillaries (Figure 6).

The walls of the capillaries show a peculiar thickening in the area of the luminous body. If it had not been frequently observed that the large, thin-walled vessels become rapidly thick-walled at their entrance into the luminous body (Figure 3) and then divide into the dense capillary network, one would hardly believe that this intricate network of winding, thick-walled canals that reveals itself on sectioning is formed by capillaries. However, there are often blood cells (*sang.*) in the lumen and their small, rounded nuclei differ distinctly from the elongate-oval or irregularly crenate nuclei of the walls of the capillaries (*nu. cap.*). Once the strange structure of the luminous body is recognized, the nuclei of the walls of the blood vessels, the blood cells and the luminous cells are easily distinguished.

The **nerves** are distinctly recognizable only in the ventral organs (Figure 2, 5, *n.*). The innervation is clearly formed by branches of the visceral nerve, which surrounds the anterior margin of the organ. A thick branch of the visceral nerve enters the gelatinous body near the entering artery and the efferent vein (Figure 2). The nerve (Figure 5) extends in the plane of symmetry of the organ along the reflector to the luminous body; it has a few lateral branches before dividing into numerous fine branches near the luminous body. These fine branches penetrate the mesh of the gelatinous body toward the luminous body and are easily recognized by their long granulated nuclei.

All organs have a **reflector** in the form of a relatively thick layer outside the luminous body. The ventral organs of *Ch. veranyi* have a particularly well-developed reflector, which consists of squamous cells with central nuclei and concentrically stratified lamellae. Toward the periphery and the luminous body, the squamous cells pass into lamellae which become loosely undulate as they approach the luminous body. The reflector of the eye organs has a fibrous structure.

The reflector of the arm organs of *Ch. veranyi* (Plate XLIV, Figure 1) is homogeneous with a few oval nuclei, while that of *Ch. imperator* has a distinct fibrous structure. In both cases it forms a cup with the convex side outward; it becomes flatter toward the musculature of the arms, assumes a more fibrous structure and then, becoming thinner, surrounds the gelatinous body.

255 The **gelatinous body** (*gel.*) is present only in the ventral and arm organs. It is a separated part of the cutis and consists of thin lamellae of connective tissue which enclose the structureless jelly in a honeycomb pattern. The crossing points of the honeycomb are thickened and there are large, light-colored connective tissue cells, filled with fluid, which show some resemblance to the cartilage cells of vertebrates (Figure 4, *bg.*). These cells are rounded, oval or spindle-shaped, and have a large nucleus from which the plasma branches through the vacuolated content of the cell. The intercellular substance stains strongly with carmine and hemalum, while the cell content, excepting the nucleus, fails to stain almost altogether. The capillaries and nerves pass on the lamellae and then through the cartilage-like tissue at the crosspoints. The capillaries are surrounded only by the light-colored cells of connective tissue but not by the intercellular substance (Figure 4, *cap.*).

In the eye organs, the gelatinous body is replaced by a striated body which extends from the reflector and from the outer margin of the luminous body (Figure 6, *b.*). It consists of long, curved, finely striated fibers. The striation is caused by the concentric stratification of lamellae (Figure 9) which contain a thin layer of protoplasm with very long nuclei (*nu.*). At the reflector these fibers pass gradually into cells consisting, too, of a system of lamellae with a nucleus.

A pigmented sheath is present only in the arm organs because its necessity is obviated—in the eye organs by the dark envelope of the eyeball, and in the ventral organs the ink sac replaces it (Figure 2, *atr.*). The sheath of the arm organs consists of numerous chromatophores which are particularly dense around the outer end of the organ, though they are present too, albeit very sparsely, in the part facing the arm musculature. Histological examination failed to provide any information as to whether the chromatophores cause a certain coloration of the light.

Polymorphism of the Luminous Organs of *Chiroteuthis*

Chiroteuthis has only 3 types of chromatophores, but their structure differs so markedly that a different quality of emitted light may be assumed.

The **arm organs** (Plate XLIV, Figure 1) form slightly raised knobs on the inner side of the ventral arms near the dorsal row of suckers. They have a radial structure and are so situated that the light emitted by them has to pass through the substance of the arm. According to Vérany (1851, p. 122), these organs have a silvery sheen seen from the outside of the arm, but when seen from the inner side, the chromatophores give them a black brown shade. The thick parabolic reflector (*refl.*) is homogeneous in *Chiroteuthis veranyi* and finely striated in *Ch. imperator*. The reflector flattens outside the luminous body into a fibrous capsule which envelops also the flattened periphery of the organ opposite
256 the luminous body. The lens-shaped luminous body (*phot.*) is situated on the thick part of the reflector at the bottom of the organ. Near the gelatinous body the luminous body contains numerous large nuclei which belong to the luminous cells, but near the reflector the luminous body consists almost entirely of a very fine capillary network (*cap.*). The main mass of the organ consists of a gelatinous tissu (*gel.*) of a much narrower mesh than the gelatinous tissue of the cutis. The larger blood vessels extend through the lamellae of connective tissue of the gelatinous body to the luminous body, mainly at the periphery but also in the center, and then form the characteristic capillary network in the area of the reflector. The organ is enveloped by a pigmented capsule, formed by large chromatophores which are stacked in several layers and are most densely arranged on the outward-facing part of the reflector.

The **ventral organs** resemble the arm organs in many respects but differ in their bilateral structure, their larger size and the absence of a sheath of chromatophores. Vérany observed these organs shining through the abdominal wall of the live animal and described them as follows: "Sur la ligne médiane on remarque une tache, en forme de coeur renversé, bleue très prononcée; sur chaque lobe de ce coeur brille un gros point à reflet métallique argenté."

This sheen is still visible in the preserved specimen; the organs of *Ch. imperator* have a more golden or coppery sheen, which derives mainly from the lateral outer side of the organ (Plate XL, Figure 7). The organs resemble a funnel with the rounded apex directed laterally; their plane of symmetry is almost perpendicular to the longitudinal plane of the body. As pigmented sheath acts the heart-shaped ink whiih surrounds the posterior side of the ventral organs and is pressed in by them.

The reflector (Plate XLIV, Figure 2, *refl.*) is well developed; it flattens gradually toward the median margin of the organ but ends truncate on the opposite side. In its middle the reflector consists of squamous cells, which gradually pass, inward and outward, into elongate fibrous cells.

The luminous body (*phot.*) is lens-shaped in *Ch. imperator* but it fills a deep, funnel-shaped pit at the apex of the reflector in *Ch. veranyi.* The capillary network in the luminous body is usually not as dense as in the arm organs. The whole space enclosed by the reflector is filled with a gelatinous tissue (*gel.*), comprising a modified part of the cutaneous tissue, as in the arm organs. In the large organs of *Ch. imperator*, the mesh formed by the lamellae of connective tissue is larger than in *Ch. verany*; in both species, however, it tends to form broad knots which contain light-colored cells of connective tissue with large nuclei (Figure 4). The ventral organs are covered on the outside by the epithelium of the abdominal wall.

The vessels (Figure 2, *art.*, *v.*) are branches of the posterior aorta and small veins which open into the vena cava. They enter at the median margin, branch repeatedly in the gelatinous tissue toward the luminous body and then pass with thickened walls into the capillary network.

257 The organs are innervated by branches of the visceral nerve which enter at the median margin together with the vessels, pass near the reflector and divide into numerous branches in the luminous body.

I examined only the **eye organs** of *Ch. imperator*. They form 3 rows on the ventral surface of the eyeball (Plate XLIII, Figure 2, *luc.*[1], *luc.*[2], *luc.*[3]). They are lens-shaped (Plate XLIV, Figure 6) and differ markedly from the organs earlier described by a frontally extended lens (*l.*), which consists of curved fibers extending radially from the anterior side of the luminous body to the periphery. The lateral fibers pass into the reflector (*refl.*), which forms a thick layer on the posterior side of the organ. The reflector consists of squamous cells with loosely arranged lamellae. In contrast to the other organs, the reflector is pervaded by blood vessels (*v.*) that form a very fine capillary network (Figure 7) inside the luminous body (*phot.*); the latter lies flatly spread between the reflector and the radial fibers of the lens.

Gladius

(Plate XLI, Figures 10–16)

The gladius of *Chiroteuthis* was only incompletely described by Vérany, who was the first to describe it at all. Verrill (1881, p. 410, Plate 56, Figure 1) gave a more exact description of the gladius of *Ch. lacertosa*, which is apparently identical with *Ch. veranyi.* His description states that it consists mainly of the rhachis at the anterior end, while the posterior end bears a wide cone. This agrees with the description of Hoyle (1886, p. 178, Plate 31, Figures 1–5), Joubin (1894, p. 54, Plate 2, Figures 10–14) and Goodrich (1896, p. 13, Plate III, Figures 52, 53). Joubin's description, however, differs markedly. According to him, the gladius consists of a closed tube its whole length and is broadly open for a short distance only at the opening of the cone.

I was able to confirm the descriptions of *Ch. imperator* by Verrill, Hoyle and Goodrich, but not that by Joubin. The following description is based on the gladius of a medium-sized specimen. It is 230 mm long (Figures 10, 11, 12), coinciding with the length of the gladius described by Joubin. The cone is 147 mm long; it begins at the level of the anterior margin of the fins and extends to the posterior tip of the body. The very fine tip of the cone was broken off in all specimens, so that its exact length cannot be given.

Compared to its length, the gladius is very narrow; it is 3 mm wide at the anterior end and only 1.5 mm wide posteriorly, just before the cone. The cone is elliptical in cross section, 5 mm wide dorsoventrally, and 3 mm laterally.

The rhachis widens gradually from the posterior end of the body to the dorsal corner of the
258 mantle, where it is also slightly flattened. The cross section resembles an open rectangle with the 3

surfaces meeting at an almost right angle (Figures 10 a, 10 b). The ventral corners of the lateral surfaces are thicker where they curve outward and continue on each side into a narrow, thin lamella—the almost suppressed vane.

The thin lamellae of the vane widen abruptly at the level of the anterior margin of the fins and are curved ventrally, become contiguous further on, and are finally fused on the ventral side (Figure 12). The vane thus forms a cone which is broadly open anteriorly on the ventral side but is completely closed posteriorly. A cross section of the cone (Figure 10 c) shows that it consists of two layers of chitin. The outer layer is dark and consists of the rhachis and the lateral wings of the cone. The inner layer is thick and light and fills the rhachis completely; this layer forms a groove at the ventral side of the cone which becomes indistinct posteriorly, at the point where the two wings are fused (Text Plate 2, Figure 4).

As already mentioned, the tip of the cone was lost in all specimens. However, numerous irregularly arranged transverse septa (Figure 13) prevent seawater from entering the inner cavity at the cone. These septa are certainly homologous to the transverse septa in the phragmocone of other Cephalopoda. They are particularly distinct if the cone is examined dry. The chambers between the transverse septa then become filled with air and appear like a string of pearls.

This description agrees in general with the not very detailed description of Verrill, Hoyle and Goodrich. Hoyle correctly considered the cone of an apparently gigantic specimen taken from the stomach of a shark in the Pacific as that of *Chiroteuthis*. The fragments are together 78 cm long, so that the complete gladius was probably 1 m long.

The description by Joubin, however, does not correspond to a normal gladius of *Chiroteuthis*. According to his description, the rhachis, too, is completely closed, and the cone has a short, slitlike opening anteriorly—a condition which would be unique among the Oegopsida. The original specimen of *Ch. picteti* which I examined had no gladius, so that I cannot decide whether the condition described is normal.

Formation of the Gladius and Topography of the Posterior Region of the Body
(Text Plate 2)

The gladius is secreted by the shell gland; the gland surfaces adhere closely to it. In the live animal and also in many points in the preserved animal, the gladius thus represents a chitin-filled negative of the lumen of the gland. Shrinkage takes place during preparation for sectioning, so that the gladius
259 appears to lie freely in a pocket formed by the shell gland. This explains the distance between the gladius and the walls of the shell gland on Text Plate 2, which shows cross sections of different parts of the gladius and its surroundings. This is especially the case in cross section 1, which is situated just in front of the cone. The shell gland (*sacc. glad.*) is more or less kidney-shaped in cross section and consists of two lamellae of epithelium which are fused laterally. The dorsal lamella (*lam. d.*) consists of pavement epithelium, the cells in the middle of the ventral lamella (*lam. v.*) are more cuboid. The findings from sections confirmed my assumption that the ventral lamella is the major participant in the secretion of the chitinous lamellae; the latter are extraordinarily thin and densely stratified.

The cross section changes markedly at the level of the cone (Figure 2), because the shell gland (*sacc. glad.*) here becomes horseshoe-shaped. At the beginning of the cone, the arms of the shell gland diverge broadly ventrally; they form the wings of the cone, while the median part secretes the rhachis.

Again, it is the inner (ventral) side (*lam. i.*) which, being lined with cylindrical epithelium, suggests greatest participation in the secretion of the cone. The cylindrical epithelium, however, does not cover the inner surface of the gland uniformly but is restricted to a dome of median cells which fill the rhachis

and, moreover, to the ventrally situated lateral surfaces which secrete the wings of the cone. In deeper sections (Figure 3), this epithelium is displaced nearly completely to the ventral side; here the arms of the shell gland approach each other so closely that they become almost contiguous in the ventral line. Finally, they meet and fuse, so that the two epithelial lamellae become separated and the originally ventrally situated lamella now becomes completely enclosed by the cone, while the dorsal lamella forms an outer cover of the cone. However, the activity of the inner lamella is not terminated. A thick layer of light-colored chitin is formed beneath the initially formed dark chitinous layer. This light layer lines the inner cavity of the rhachis and the lateral and ventral walls of the cone, and constricts the lumen of the cone (Figure 4).

The above processes of the formation of the cone are not difficult to understand. However, it is hard to explain the formation of the thin septa at the posterior end of the cone. For a clarification of these conditions it is necessary to describe the **topography of the posterior end of the body** with special reference to the surroundings of the cone.

The cross sections on Text Plate 2 were made from a young specimen fixed in formol. The drawings are slightly diagrammatic in order to correct irregularities caused by shrinkage.

Some of the most prominent formations near the cone (Plate XLI, Figures 14–16) are thick, dorsally passing pallial nerves (*n. pall.*). They are surrounded by a thick envelope of connective tissue which contains two vessels, a median artery and an outer vein. These nerves are situated on each side of the
260 gladius in front of the cone (Text Plate 2, Figure 1, *n. pall.*); but they are displaced dorsally in the area of the cone (Figure 2), from where they chiefly supply the fins with thicker lateral branches.

The large abdominal veins pass ventrally below the broadly open wings in the beginning of the cone (Figure 2, *v. abd.*) and are later displaced more dorsally (Figure 3, *v. abd.*). These veins receive the small veins near the pallial nerves at the level of the anterior part of the cone and also some smaller vessels which branch in the area of the cone (Plate XLI, Figures 15, 16).

The posterior aorta (*a. post.*) passes on the median ventral surface of the posterior part of the mantle. It then divides into two lateral branches which turn dorsally and continue posteriorly more or less parallel to the abdominal veins. These branches could be named "fin arteries" (*a. pinn.*), since they supply blood mainly to the musculature of the fins.

The tissue inside the cone is of particular interest. To explain its topography we have to refer to the gastrogenital ligament—the cord which extends from the stomach and from the genital gland adjacent to it. Young specimens have a short, thick gastrogenital ligament which extends at the dorsal surface almost perpendicular to the longitudinal axis of the body (Plate XLI, Figure 20, *lig. g. g.*). In older specimens, this ligament is thin, 12–15 mm long, usually with a trumpetlike widened end which is attached in front of the cone. Cross sections of the anterior part show that it is a strong cord of longitudinal muscles and contains a small artery, apparently a continuation of the gastric artery. Gelatinous connective tissue appears on the widened distal part on which the longitudinal muscles are situated ventrally. These muscles are divided directly in front of the cone in the form of a crescent and then continue in the lateral tissue (Plate XLI, Figures 14, 15, *mu.*).

The gelatinous tissue, in which the gastrogenital ligament ends, is swollen near the opening of the cone into a large pad (Figures 14–16, *x.*) which protrudes like a hernia from the opening of the cone and extends markedly into the end of the mantle cavity (Plate XLIII, Figure 1, *gel. con.*). I considered this structure at first as a dilatation of the arterial vessel and assumed that it is a kind of heart of the fin. However, this is only gelatinous tissue which fills the opening of the cone. This tissue appears in cross section (Text Plate 2, Figure 2) as a pad which protrudes between the two arms of the cone. The following sections show that this tissue is gradually surrounded by the ventral wings and finally becomes com-

pletely enclosed by the cone (Figure 3). It forms a long tube inside the cone which extends almost to its tip and can be removed without difficulty from the lumen. This tube is covered with epithelium which secretes the inner chitinous lamella of the cone. This is obviously the inner (ventral) epithelial lamella of the shell gland, i.e. the lamella which becomes separated from the outer lamella at the time of closure of the cone (p. 202). The tube consists mainly of the characteristic connective tissue that has a
261 honeycomb pattern of lamellae which include a structureless hyaline jelly (Plate XLI, Figure 13). In the lamellae are numerous capillaries which originate from two larger vessels—a vein passing dorsally and an artery passing ventrally (Text Plate 2, Figure 3, *art.v.*). Joubin (1894, p. 55) noted this tube and stated correctly that it consists of a gelatinous connective tissue which is enclosed by an epithelial layer and contains numerous capillaries. However, he failed to notice the larger vessels which extend dorsally and ventrally as arteries and veins. The soft body enclosed by the cone does not reach to the tip of the gladius but rounds off and ends a good way before the tip (Plate XLI, Figure 13). This condition is apparently caused by the formation of the thick chitinous layer on the inner wall of the cone, gradually causing a marked narrowing of its lumen. The pressure thus created forces the enclosed soft parts toward the anterior, where the lumen gradually widens, so that it accommodates them. The stages of this retraction during the lengthening of the gladius are indicated by the formation of transverse septa. These are secreted by the epithelium which covers the posterior end of the inner tube and are of rather irregular form; it would seem that only the thicker septa close the cavity of the cone against the entry of seawater.

Finally, some remarks on the arrangement of the gelatinous tissue of the mantle in the vicinity of the cone. The mantle consists mainly of a honeycomb pattern of lamellae which generally show a radial arrangement and form the support for radial or diagonal muscular fibers, thinner branches of nerves and capillaries. The lamellae include a homogeneous structureless jelly. This gelatinous layer is covered on the outside with a thin layer of longitudinal muscular fibers (Text Plate 2, Figure 2, *mu.long.*)*; its inner surface is covered with the circular system of fibers which surround the respiratory cavity. Outside the longitudinal muscles is the cutis (*cut.*) which, too, adheres to its chromatophores (*chr.*) by means of a gelatinous mass.

The gelatinous tissue around the cone is especially tough and small-meshed. It forms an elastic, resistant pad which stiffens the outer lamella of the shell gland and forms the base for the attachment of the fin musculature at the level of the rhachis (Text Plate 2, Figures 2, 3, *cart.pinn.*)**. The lamellae of connective tissue form a network and their nodes become wider and resemble cartilage. This is in fact the fin cartilage, having pale, rounded or oval cartilage cells, set off by the more strongly stained elastic intercellular substance. At the posterior end of the body, where the respiratory cavity has disappeared (Figure 3), this cartilaginous tissue also surrounds the ventral side of the cone. From this area extend especially tough, radially arranged lamellae, particularly two distinct lateral lamellae. These lamellae form a kind of transverse septum behind the fins which extends from the ventral margin of the cone (Text Plate 2, Figure 5) and divides the systems of lamellae into a broad, flat dorsal system and a curved ventral system.

* [Seems, however, to have been omitted in the author's drawing.]

** [This, too, is not specified in the author's drawings.]

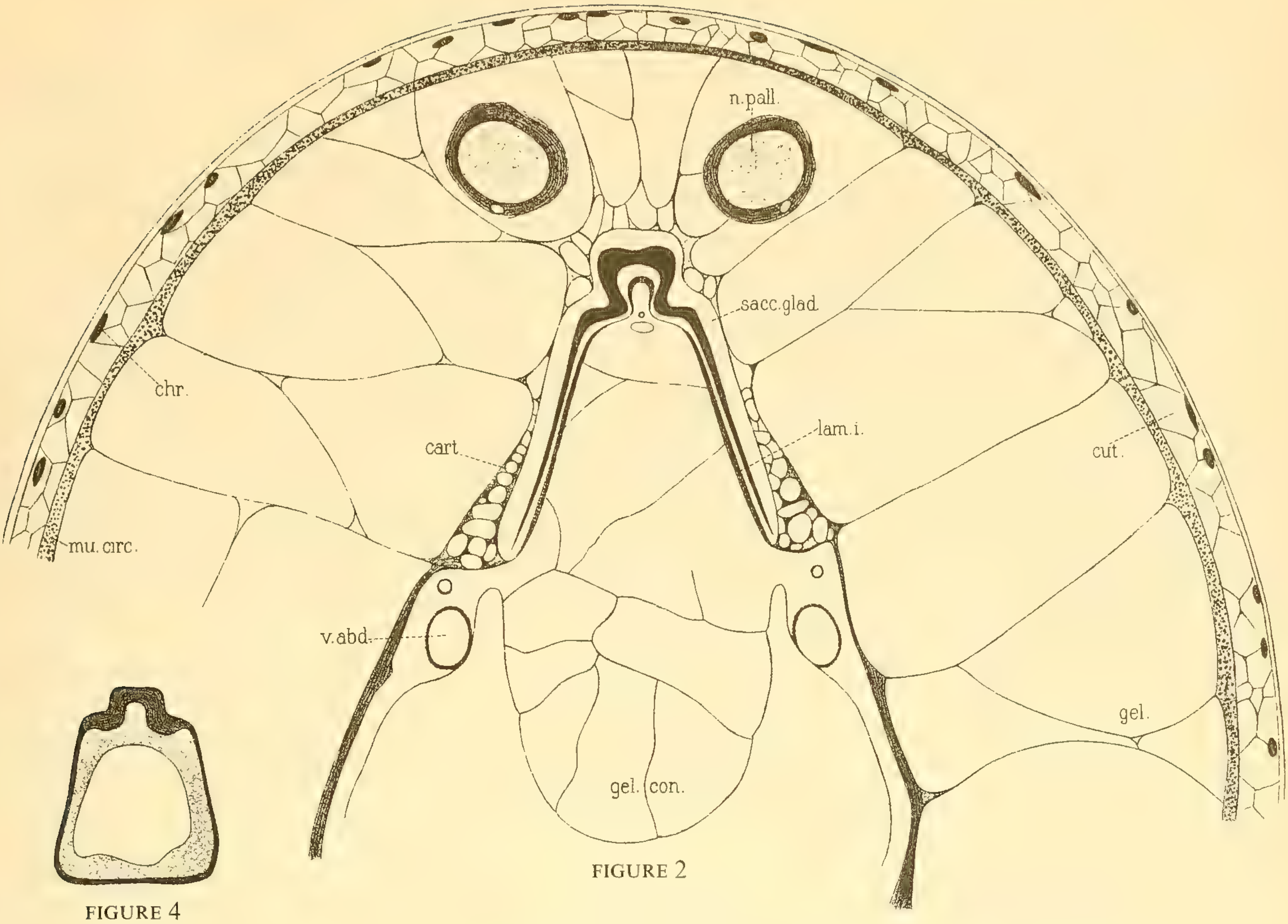


FIGURE 2

FIGURE 4

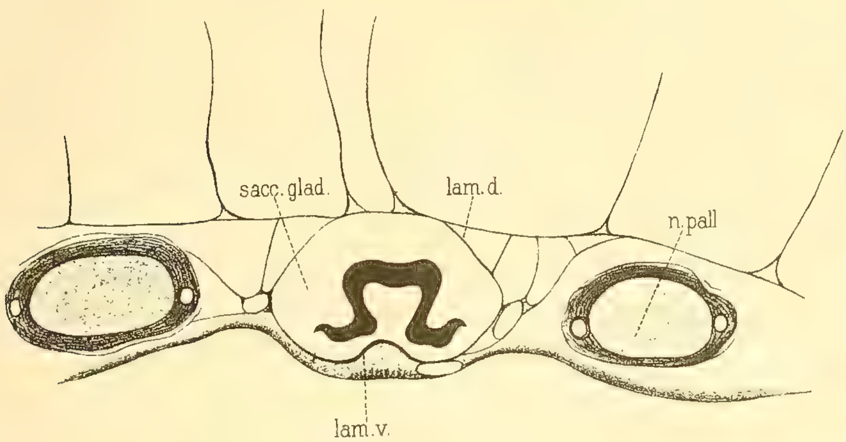


FIGURE 1

FIGURE 5

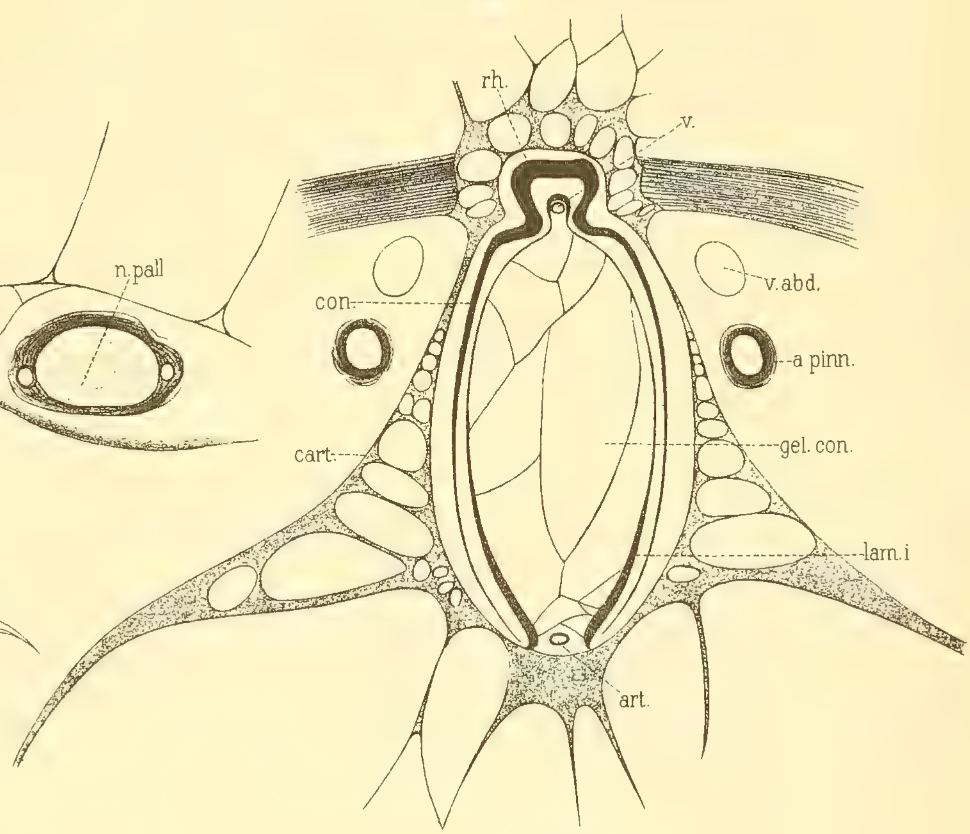


FIGURE 3

TEXT PLATE 2

Chiroteuthis imperator. Gladius and posterior end of the body

262 ## Anatomy of the Inner Organs

MANTLE COMPLEX

Opening of the mantle cavity from the ventral side (Plate XLII, Figure 1) shows a septum (*sept.*) which is displaced far posteriorly between the mantle and the ventral surface. The pallial artery, which branches from the posterior artery, passes along the anterior margin of this septum.

The organs of the mantle cavity border anteriorly on the posterior margin of the funnel (Plate XLIII, Figure 1) which passes across the anus, so that the funnel must also be opened to show the whole complex. This also exposes the funnel organs and the funnel valve, which have already been described. Along the dorsolateral side of the funnel passes the funnel depressor (*mu. depr. inf.*), which begins as a fine cord in front of the base of the gills and widens like a fan toward the anus and toward the funnel cartilage. This muscle forms a thin lamella and its median margin is fused with the liver sac.

The anterior part of the mantle complex contains the long liver on the median part of which are situated the looped mid-intestine and the rectum. The anus is bordered by two lips with relatively small lateral appendages. Beneath the mid-intestine and the rectum is the ink sac the dilated heart-shaped posterior part of which forms the substrate and pigmented envelope for the two large ventral luminous organs (*luc.*). These are distinguished by their golden or coppery metallic sheen and the honeycomb pattern on the surface (Plate XL, Figure 7).

Behind the luminous organs extends the anterior margin of the renal sac which occupies the middle of the mantle complex. The outer openings of the renal sac are slightly projected in chimney form; they are situated just behind the ventral organs (Plate XL, Figure 7, *ur.*). The large venous appendages are visible through the thin ventral abdominal wall; removal of the whitish coagulate from the sac shows the vessels which extend from the posterior artery and branch on its ventral wall, forming two larger vessels for the luminous organs.

The renal sac covers laterally the oval branchial hearts (*c. branch.*) and the base of the gills. The latter are well developed and form a slender pyramid which is 32 mm long in the large specimen. There are 28 lamellae in an alternating arrangement on each side of the gill; the outer lamellae, i.e. those near the mantle, are larger than the inner lamellae. The branchial gland is therefore visible only on the inner side. It is 7 mm wide and ends in a strong, narrow ligament which attaches the gill to the mantle.

On the ventral side of the gill passes the branchial vein, which widens markedly at the base and receives the efferent vessels of the branchial lamellae. The vessels are often turgid with whitish coagulated
263 blood. The posterior part of the mantle complex is enclosed by the thick abdominal wall. On its median ventral side passes the posterior aorta, on the lateral surfaces, the large abdominal veins which usually shine through (*v. abd.*).

The two nidamental glands (*nid.*) are readily visible in females; not quite as readily are the nearly covered openings of the oviducts (Plate XLII, Figure 1) visible near the base of the gills. The spatulate duct of the spermatophore sac of the male is present only on the left side.

CRANIAL REGION

Opening of the head from the dorsal side reveals in its middle the large, smooth-walled roof of the cranium (Plate XLIII, Figure 3, *cran.*) which covers the brain, except for the superior buccal ganglion (*g. bucc. sup.*) and for the arm ganglion which is covered by the superior buccal ganglion. It appears at first as if there is a large cartilaginous cranium, but further preparation shows that the anterior part of the cartilaginous cranium forms a broad, dish-like hemispherical roof which covers the optic ganglia

and the white bodies. In the heart-shaped indentation of the posterior side there are the posterior salivary glands (*saliv. post.*) with their dorsal groove, which contains the esophagus (*oes.*), the aorta (*a. ceph.*) and the pallial nerves (*n. pall.*). The salivary duct at the base of the heart-shaped indentation and the above structures all pervade the thick posterior surface of the cranium.

The cranium thus contains the brain and the static organs and its form is markedly influenced by the large eyes, which compress the anterior median part to a narrow plate, having a sharp concave margin and passing behind the superior buccal ganglion (*g. bucc. sup.*) and the arm ganglion (*g. brach.*) (Plate XLI, Figure 4, *m. cr.*) and then widening dorsally and ventrally like a wing. These cranial wings surround the posterior surface of the eyes as far as they are covered by the optic ganglion and the white body (Plate XLIII, Figure 4). The supraorbital muscles are attached on the flattened upper anterior margin of the wings, the infraorbital muscles on the lower margin.

The compressed median part of the cranium near the sides of the brain is not cartilaginous but consists of thin lamellae of connective tissue, through which the brain is visible. Opening of the orbit (Plate XLI, Figure 4) shows that the cartilaginous margin of the median part of the cranium (*m. cr.*) begins in a sharp curve just before the pedal ganglion (*g. ped.*), passes below it and the visceral ganglion (*g. visc.*), and then surrounds the optic nerves on the dorsal side. The median part of the cranium thus forms on both sides a wide, rounded indentation which is enclosed by thin lamellae of connective tissue. These lamellae surround the brain and are perforated by the optic nerve. Two muscles also surround the sides of the brain; they originate on the ventral anterior margin of the indentation and extend like a fan toward the dorsal margin to the optic nerve (*mu. flab.*).

Below the indentation is a foramen, which perforates the cartilage at the level of the pedal ganglion. A muscle, originating before the foramen, extends to the eyeball.

264 The ventral posterior part of the cranium is laterally inflated by the static organs; its base is penetrated by the vena cava (*v. c.*), which forms a caecum (*s. v. c.*) at the exit from the cranium (Plate XLIII, Figure 2).

The **static organs** (Plate XLI, Figure 5, *o. stat.*) are enclosed by a thick cartilaginous wall; they are innervated by the divided nervus staticus, which originates in the brain. The cartilaginous wall is funnel-shaped, and in longitudinal section, obtuse-triangular. The cartilage forms two ridges which project against the thin-skinned organ; one of them passes in a curve on the outer side (Figure 5 shows this ridge in cross section), the other extends on the inner side, more or less perpendicular to the former. There are also cartilaginous processes of varying size which project inward. The static organ of a larger specimen contained 13 such processes, 7 on the inner side, 6 on the outer side. The static organ of a medium-sized specimen had only 8 processes arranged in two rows of four.

The head and neck behind the cranium contain oblique septa which form 7 pocketlike spaces in the largest specimen.

NERVOUS SYSTEM
(Plate XLI, Figures 1–9).

If the nervous system of *Chiroteuthis* has received my special attention, it was for the following reasons: Primarily it appeared desirable to choose precisely a primitive form among the 10-armed Cephalopoda as starting point for a more detailed study of the nervous system. I have already stressed that the Oegopsida show more primitive conditions than the Myopsida. On this point, especially as regards the nervous system, my views clash with those of Ihering (1877, p. 260), who believed that the nervous system of the Oegopsida (as described by Hancock, 1852) shows the most aberrant condition and attempted to prove that the concentrated nervous system of the Octopoda shows

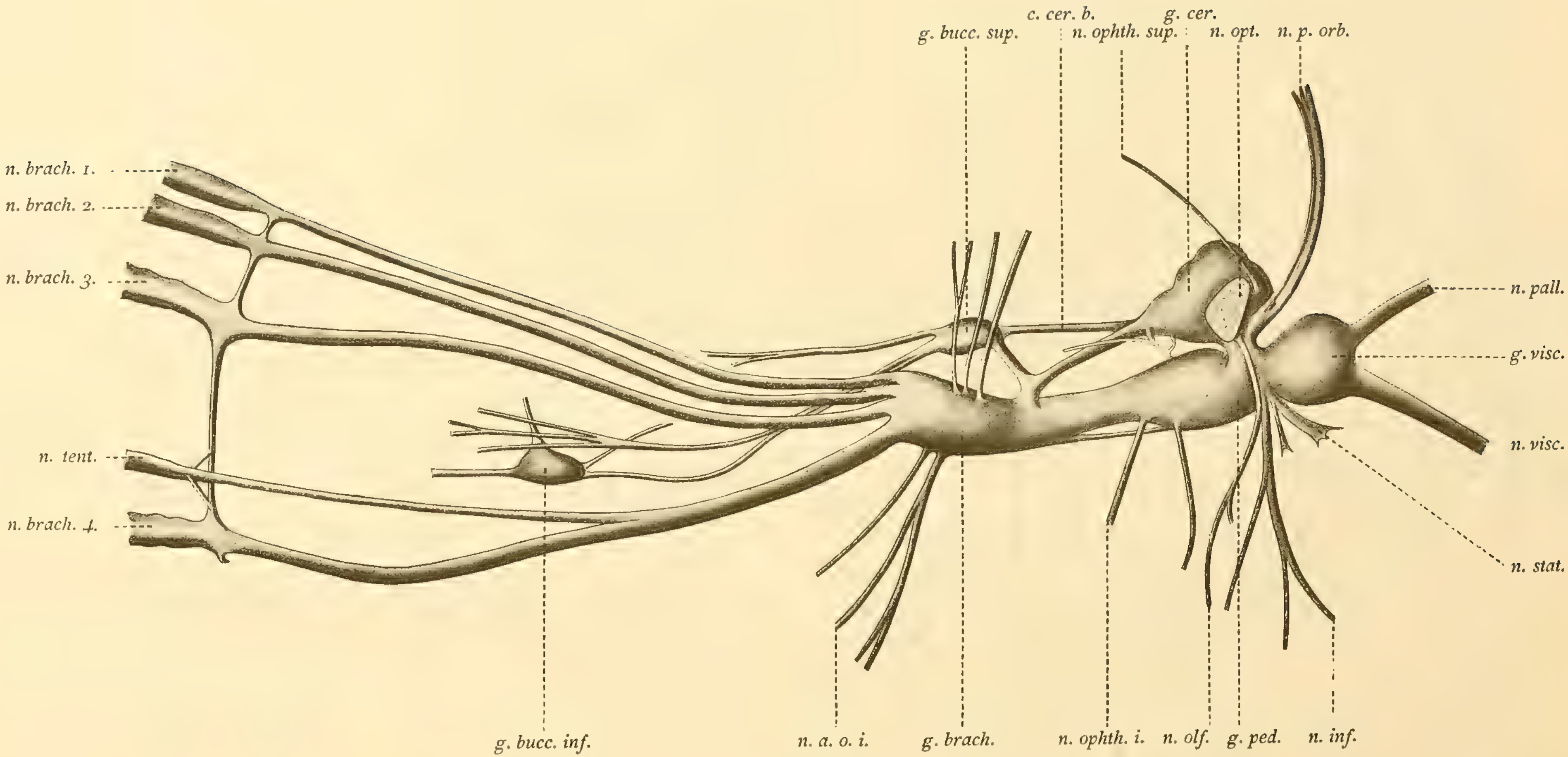


FIGURE 28. Nervous system of *Chiroteuthis imperator*, lateral view:

g. cer. cerebral ganglion; *g. brach.* brachial ganglion; *g. ped.* pedal ganglion; *g. visc.* visceral ganglion; *g. bucc. sup.* superior buccal ganglion; *g. bucc. inf.* inferior buccal ganglion; *c. cer. b.* cerebro-buccal commissure. Nerves originating from the cerebral ganglion: *n. opt.* optic nerve; *n. olf.* olfactory nerve; *n. ophth. sup.* superior ophthalmic nerve; *n. p. orb.* postorbital nerve. Nerves originating from the pedal ganglion: *n. inf.* funnel nerve; *n. stat.* nerve to the statocyst; *n. ophth. i.* inferior ophthalmic nerve. Nerves originating from the visceral ganglion: *n. pall.* pallial nerve; *n. visc.* visceral nerve. Nerves originating from the brachial ganglion: *n. brach. 1, 2, 3, 4* the 4 nerves to the arms; *n. tent.* nerve to the tentacle; *n. a. o. i.* inferior antorbital nerves (the superior antorbital nerves originate at the level of the superior buccal ganglion).

the most primitive conditions. I do not believe that Ihering still maintains this position, in view of recent studies on the anatomy and morphological variety of the Oegopsida. In my opinion the very opposite is true: the most aberrant conditions are found precisely in the Octopoda, with their marked concentration of the various centers, these conditions reaching their extreme, in turn, in the most aberrant group—the Cirroteuthidae.

Another reason for this study was the lack of contributions to our knowledge of the nervous system of the Oegopsida, which has made no progress since the work of Hancock, and that is certainly not free of any errors. The nervous system has been described occasionally but not as thoroughly as by Hancock. However, some later data, particularly by Appellöf (1889, 1890), deserve attention because they contain new data.

266 My choice of *Chiroteuthis* for a description of the nervous system rests on the fact that this is a large representative of a very characteristic family of Oegopsida, with a long anterior part of the body in which a distinct development of the central nervous system may be assumed. One specimen was used for this study and other details were confirmed in a second specimen. Of great value for the detailed preparation was the Zeiss binocular magnifying lens, which permitted deep penetration. However, no information on the microsopical structure of the ganglionic centers should be expected, since such a study requires more abundant material, fixed especially for this purpose.

Ganglionic Centers and Commissures

The nervous system of *Chiroteuthis* consists of 4 centers: the ganglion cerebrale, which is situated above the esophagus; the ventrally situated ganglion brachiale; the ganglion pedale; the ganglion viscerale. There are also the upper and lower esophageal ganglia, i.e. the ganglion supraoesophageum (buccale superius) and the ganglion infraoesophageum (buccale inferius). All these ganglionic centers are distinctly separated and lie particularly wide apart in *Chiroteuthis*. Due to this condition, the origin of the nerves which originate on these ganglia can be determined more accurately than in the Myopsida or Octopoda.

The **ganglion cerebrale** (optic ganglion of Hancock) is pear-shaped and consists of 3 or 4 parts (Figure 5, *g. cer.*). Its highest elevation is dome-shaped and divided by a median groove (Figure 1). In front of the groove there is a conical part with slightly swollen apex. This part also consists of two divisions: on the anterior part originate the commissures, and the posterior part adheres closely to the divided dome. Finally, there is a steeply sloping posterior part without a median groove.

Commissures connect the ganglion cerebrale with the ventral ganglia and with the supraesophageal ganglion. The ganglion opticum covers a large commissure which connects it on each side with the ganglion pedale. This commissure is not very wide and extends obliquely backward, in the form of a band, below the optic nerve (Figure 4, *c. cer. ped.*). From the conical anterior apex originates a second unpaired commissure (Figures 1, 4, 5, *c. cer. b.*) which extends to the ganglion supraoesophageum and becomes divided further on.

In both specimens examined I found in front of the thick commissure a weakly developed commissure which connects the ganglion cerebrale with the ganglion pedale. It begins with two united roots on the anterior part of the ganglion cerebrale and extends to the dorsal side of the ganglion pedale (Figure 5). This commissure sends out a thin nerve to the muscular lamella; the latter pervades the orbit in a fan-like spread out manner.

The **ganglion pedale** ("medial suboesophageal mass" of Hancock) is oval and situated directly
267 below the brain (*g. ped.*), is nearly as long as the brain, and forms anteriorly a single, broad commissure

which connects it with the ganglion brachiale. This large commissure (I name it "bridge commissure") may be considered as a special part of the brain. However, it apparently contains only fibers but no ganglionic components.

The **ganglion viscerale** (*g. visc.*) is situated immediately behind the ganglion pedale. In the large specimen from Station 194, an indistinctly differentiated tract extends from the lateral wall of the ganglion viscerale to the ganglion cerebrale. The ganglion viscerale is almost spherical in lateral view and not longer than the ganglion cerebrale. The ganglion viscerale consists of 3 parts: two paired upper parts, which may be named pallial ganglia, and a single lower part which represents the ganglion viscerale in the strict sense. Hancock distinguished between these parts and named the paired swellings "ganglion branchiale" and the single ventral part "ganglion viscerale."

The **ganglion brachiale** (*g. brach.*) is longer than the above centers. It forms a blunt triangle which broadens anteriorly and the thick nerves of the arms originate on its anterior part. A wide, shallow groove on its dorsal side supports the organs which pass through the brain (intestine, vena cava, arteria buccalis and salivary duct). Commissures (*c. cer. br.*) extend obliquely on each side from its posterior end to the ganglion cerebrale. From the same root originate other commissures (*c. brach. b.*) which extend obliquely anteriorly to the ganglion supraoesophageum. These commissures form a scalene triangle with the commissure that connects the brain with the ganglion supraoesophageum (*c. cer. b.* in Figure 5).

Finally, a thin accessory commissure connects on each side the posterior end of the ganglion brachiale with the anterior end of the ganglion pedale. This paired commissure is situated ventrally below the wide bridge commissure (Figure 5).

Thus, the following commissures originate from the ganglion brachiale:

1. Commissura brachio-pedalis (bridge commissure);
2. Commissura brachio-cerebralis;
3. Commissura brachio-supraoesophagea;
4. Commissura ventralis (brachio-pedalis accessoria).

The **ganglion supraoesophageum** (ganglion buccale superius) is almost as broad as the ganglion cerebrale (*g. bucc. sup.*) but much shorter. It is more or less crescent-shaped in dorsal view and slightly concave anteriorly (Figure 1). This ganglion is situated unusually far from the brain, above the ganglion brachiale. The following commissures connect it with the adjacent ganglionic centers:

1. Commissura cerebro-supraoesophagea (*c. cer. b.*):
This commissure originates on the anterior apex of the ganglion cerebrale as a single, laterally compressed band which is divided behind the unpaired esophageal ganglion. It has been described similarly by Hancock (1852, p. 2, Figure 2) for *Ommatostrephes*. According to Appellöf (1890, p. 6), this commissure originates in *Chaunoteuthis* on the brain as a double, not a single, cord.

268 2. Commissura brachio-supraoesophagea (*c. brach. b.*):
This has already been described in connection with the ganglion pedale.

3. Commissura supraoesophagea-infraoesophagea (Figures 1, 2, 5, *c. b. s. i.*):
These commissures connect the supraesophageal and infraesophageal ganglia. In no other Cephalopoda is their length as extreme as in *Chiroteuthis*. They are paired from the beginning, originate on the lateral anterior margins of the supraesophageal ganglion and extend to the posterior margin of the infraesophageal ganglion (Figure 2). They branch in their course into

fibers to the musculature in the suprapharyngeal area (*n.s.phar.*). These fibers may unite into independent nerves, as will be shown later.

The **ganglion infraoesophageum** (ganglion buccale inferius) (*g.bucc.inf.*) borders on the posterior ventral side of the pharynx. It is as broad as the brain but shorter and crescent-shaped, with concave anterior margin (Figures 1, 2). Because of the neck-like lengthening of the anterior part of the head, this ganglion is situated unusually far from the supraesophageal ganglion, and this causes the extreme length of the commissures which connect the two ganglia.

The most important character of the ganglionic centers of *Chiroteuthis* is the protraction and unusually large distance between the anterior ganglionic centers. Hardly any other cephalopod surpasses *Chiroteuthis* in this respect. This condition in *Chiroteuthis* is caused by the marked lengthening of the head, but in view of the general organization of *Chiroteuthis*, this feature should be regarded as primitive. Contrary to the views of IHERING, this is certainly not a secondary condition, representing, in a way, extreme development of the nervous system of Cephalopoda.

The nervous system of *Chiroteuthis* shows an unmistakable resemblance to that of *Ommatostrephes*, which was described by HANCOCK. As in *Chiroteuthis*, the ganglion brachiale and the ganglion pedale of *Ommatostrephes* are widely separated and are connected by a broad bridge commissure. The form of the brain and the ganglion viscerale are also distinctly similar in both genera.

Peripheral Nervous System

NERVES OF THE GANGLION CEREBRALE

Besides the above described commissures, there also originate five paired nerves on the ganglion cerebrale.

1. Nervus opticus. The optic nerve originates above the commissura pedalis as a very short, thick nerve which is bluntly-triangular in cross section (Figure 4, *n.opt.*). Because of the large eyes,
269 which almost border on the brain, the optic nerve is very short and passes directly into the ganglion opticum. The large development of the eyes is reflected in the large optic ganglion (Figure XLIII, Figure 4, *g.opt.*), which is 2.5 times as long as the brain and is situated in the form of a flattened blunt triangle on the upper posterior inner side of the eyeball. The two optic ganglia are situated on each side of the brain and converge anteriorly, so that they are almost continuous.

2. Nervus olfactorius. The olfactory nerve (Figure 5, *n.olf.*) originates on the ventral posterior margin of the opticus at the point where it enters the ganglion opticum. It forms a slight swelling which has to be regarded as the ganglion olfactorium. It then passes along the eyeball toward the posterior orbital margin after having given off 2 forking branches which pass in the subcutaneous tissue to the musculature of the posterior orbital margin. The olfactory nerve penetrates the cranial capsule and is markedly swollen to its end in the olfactory tubercle.

HANCOCK described the spherical ganglion olfactorium of *Ommatostrephes* (p. 8) which is situated on the ganglion opticum, the latter being slightly longer in that genus, but he does not mention the olfactory nerve which originates in this ganglion. APPELLÖF (1890, p. 7, Plate IV, Figure 15),

too, stated that there are two distinctly differentiated olfactory ganglia at the posterior part of the cerebral ganglion of *Chaunoteuthis*.

3. Nervus ophthalmicus superior. This nerve originates on the posterior lateral wall of the ganglion cerebrale at the level of the posterior margin of the nervus opticus, ascends obliquely anteriorly above the ganglion opticum and the white body, and innervates the dorsal surface of the eyeball. It is easily recognized if the dorsal cover of the cartilagineous cranium is removed (Figures 1, 5; Plate XLIII, Figure 4, *n. ophth. sup.*). Near this nerve passes the arteria ophthalmica.

Chéron (1866, pp. 45, 55) thinks that the nervus ophthalmicus superior of *Sepia* and *Loligo* belongs to the nerves which originate on the lower pairs of ganglia, especially on the ganglion viscerale. This is not the case in *Chiroteuthis*, in which this nerve definitely originates on the posterior lateral halves of the cerebral ganglion.

4. Nervi postorbitales. This is the name which I give to two nerves, a smaller anterior and a thicker posterior one, which originate on the posterior margin of the brain below the nervus ophthalmicus superior (Figure 5, *n. p. orb.*). In the older specimen from Station 194 these nerves originate on the lower side of the brain, but in a younger specimen they originate at the border between the ganglion cerebrale and the ganglion viscerale. Both nerves pass through the cartilage of the cranium, then branch and pass anteriorly and dorsally to innervate the musculature on the dorsal part of the cranium and on the eyes.

Hancock (p. 8) described two nerves, one of which apparently corresponds to the nervus ophthalmicus superior, the other perhaps to the nervi postorbitales. These nerves may be homologous with the nerve named by Chéron "nervus accessorius pallialis" and it is possible that in the higher forms they are situated completely in the area of the ganglion viscerale.

270 **5. Nervus flabellaris.** This thin nerve originates on each side of the accessory commissure between the ganglion cerebrale and the ganglion pedale and extends to the fan-like radiating septal muscles. Only in a smaller specimen was I able to trace this nerve distinctly.

NERVES OF THE GANGLION PEDALE

All nerves originating on the ganglion pedale extend ventrally and are motor-nerves, but one is a typical sensory nerve:

6. Nervus ophthalmicus inferior. It originates at the anterior lower margin of the ganglion pedale (*n. ophth. i.*) and extends in a broad band to the ventral side of the eyeball, which it innervates. It was not mentioned by Hancock.

7. Nervus oculomotorius. A small nerve which originates behind the nervus ophthalmicus inferior (*n. o. m.*) and extends to a small muscle on the inner ventral side of the eyeball.

This nerve, too, was not mentioned by Hancock, but Chéron (Plate 5, Figure 50) illustrates a double nervus ophthalmicus inferior in *Loligo*, although he fails to mention it in the text; a nervus oculomotorius is thus possibly present.

8. Nervus infundibuli. The funnel nerve (*n. inf.*) is the largest of all nerves which originate on the ganglion pedale; the latter, therefore, is sometimes named ganglion infundibuli. It originates on the posterior ventral margin of the ganglion pedale, immediately penetrates the cranial cartilage, and gives off a thick branch (*n. inf. orb.*) to the lower posterior orbital margin. Next, it passes along the anterior

margin of the static capsule, gives off a thin branch to the caecum of the vena cava and then a thicker branch to the musculature of the ventral pillars of the head. Finally, there is a moderately thick branch which innervates the musculus adductor infundibuli (Figure 9). The latter two branches pass along the wall of a depression, which forms a bowl and is equipped with chromatophores, in which the caecum of the vena cava is situated. Further on, the funnel nerve accompanies the vena cava on both sides and has a branch which extends posteriorly to the two arms of the vena cava that surround the salivary gland (Figures 5, 9). At its root, there is a thin, long nerve which continues anteriorly on the vena cava. The main branch of the funnel nerve then extends to the base of the funnel, where it forms two branches; one of them innervates the musculus collaris, the other the musculature of the funnel.

Only Hancock (p. 3) mentioned the funnel nerve of the Oegopsida as a simple thick stem. Chéron (pp. 51, 56) described a double nerve for the Myopsida, the nervus infundibuli anterior and posterior. However, his drawings are not clear and there is confusion in the lettering of the figures.
271 In respect to the indication of a special nerve for the vena cava, however, Chéron's data are definite. As far as this point is concerned, the large funnel nerve apparently also innervates the vena cava in *Chiroteuthis*. In one of the specimens, however, I found a very thin nerve which is situated between the funnel nerve and the static nerve and can be followed to the point where the vena cava enters the cranium. The fine nerve possibly becomes larger in the Myopsida, mainly innervating the vena cava.

9. Nervus staticus (acusticus). The nerve (*n. stat.*) which innervates the static organ originates directly behind the funnel nerve and divides immediately into two branches, of which the anterior is much smaller than the posterior one (*n. stat'.*). The anterior branch extends to the anterior side of the static organ, the posterior one divides into a few short branches on the lateral outer side of the static organ.

The static nerve has been mentioned by Hancock and other authors, but not its branching and its small anterior branch.

NERVES OF THE GANGLION VISCERALE

10. Nervus visceralis. The large visceral nerve (*n. visc.*) originates at the lower swelling of the ganglion viscerale as long, single stem which is as thick as the pallial nerve. It curves downward to the vena cava and then continues along it and always dorsal to it. It remains undivided through the whole neck region to near the anus, where it splits off into two branches (Figure 1) which accompany the vena cava on each side. These branches give off thin nerves to the funnel depressors behind the funnel organ. The two branches are connected by a long, looped commissure (*c. visc. a.*) behind the anus. A branch from this commissure divides into two cords (*n. atr.*) which take a winding course on the ink sac between the luminous organ and the rectum and innervate the large abdominal luminous organs. The main branches of the nervus visceralis accompany the vena cava where it passes on the right side around the liver and are connected by a second short commissure (*c. visc. p.*) at the level of the posterior margin of the right luminous organ. Close behind this second commissure the two branches divide again into two cords. The anterior of these cords, the nervus branchialis (*n. branch.*), is superficial and gives off at first 2 or 3 thicker branches to the ventral wall of the renal sacs, the anterior branch passing just before the renal papilla. The nervus branchialis then gives off a thin, forked nerve to the oviduct, just before the gill (Figure 7), and further on a thin branch to the oviduct gland, directly before the ganglion branchiale (Figure 8). The oblong branchial ganglion (*g. branch.*) is situated at the level of the oviduct gland and covered by it in dorsal view. From this ganglion extends a branch to the branchial heart (Figure 8, *n. c. branch.*), while the main nerve continues along the anterior margin of the gill (Figure 7).

272 The two deeper branches pass between the venous appendages and form an oblong ganglion near the beginning of the mid-intestine and the pancreas which I name "ganglion splanchnicum" (Figure 1, *g. spl.*). In the second specimen examined it appears as a fascicle of fibers from which branches extend to the ink sac and mid-intestine.

Hancock and Appellöf correctly described the nervus visceralis of the Oegopsida as a nerve which is single at the base and later divides into branches. The anterior commissure was described by Appellöf in *Veranya* and *Chaunoteuthis*; he also described the nerves which extend from this commissure (1889, p. 19, Figure 22; 1890, p. 11, Plate IV, Figure 16). Hancock considers the posterior commissure to be a ganglion situated on the vena cava; according to Appellöf, this commissure is represented in *Chaunoteuthis* by a direct union of the two branches into a single stem which later forks again. The posterior commissure is homologous with that described by Chéron (pp. 50 and 57) in the Myopsida, while the anterior commissure is apparently represented by two crossing and partly communicating nerves, as described by Chéron for *Loligo* (p. 57, Plate III, Figure 25). There are no clear data on the nerves which originate on these branches and extend to the gills and viscera. There is also no mention of the thickening which I named ganglion splanchnicum and which has to be distinguished from the ganglion gastricum (see below).

11. Nervus pallialis. The mantle nerves (*n. pall.*) originate on the upper lateral swellings of the ganglion viscerale with thick stems which pass near the esophagus and can readily be traced to the neck cartilage (Plate XLIII, Figures 3, 4) underneath whose margins they shine through. Shortly before the ganglion stellatum they pass to the mantle. The ganglia stellata of the medium-sized specimen lie about 14–15 mm behind the anterior end of the gladius, those of the large specimen, 22 mm. They are connected by a transverse commissure (Plate XLI, Figure 3) which was first described by Delle Chiaje and was also described by Hancock. Each ganglion sends off 5–7 repeatedly branching nerves to the mantle and none of these nerves is reunited with the main stem.

This condition is the most primitive among all Oegopsida examined. According to Appellöf (1890, p. 10, Plate IV, Figure 13), the nervus pallialis of *Chaunoteuthis* is detached from the ganglion stellatum, which is connected with the main nerve by an upper and a lower stem—the outer pallial nerves (after Brock). I am able to confirm Appellöf's data in a specimen of *Chaunoteuthis*. Brock (p. 42) maintains that the same condition is present in *Enoploteuthis*, *Ommatostrephes*, *Onychoteuthis* and especially in *Chiroteuthis*. Regarding the latter, however, I must emphasize that this is not the case.

Posteriorly the main branches of the nervus pallialis extend more or less parallel, without becom-
273 ing thinner. They reach the area of the cone on the dorsal side of the gladius (Figures 15, 16) and innervate the large fins. If the body cavity is opened from the ventral side (Plate XLIII, Figure 1), these thick stems appear strange, but this is explained by the strong development of the musculature of the fins. Cross sections of the pallial nerves (Text Plate 2, Figures 1, 2) show that they are surrounded by a thick sheath of connective tissue in which passes a larger arterial vessel. The pallial nerves also give off branches to the mantle musculature.

Nerves of the ganglion brachiale

12. Nervi brachiales. Four large nerves (*n. brach.*^{1} . . . *n. brach.*^{2}) originate on each side on the anterior margin of the arm ganglion. The nerves nearest to the median plane are the ones most strongly developed (Plate XLI, Figure 5; Plate XLIII, Figure 4). These 8 nerves innervate the arms; they include

the nerve of the tentacles (*n. tent.*) which later branches off from the nerve to the ventral arms. This condition is particularly remarkable; it explains why the common stem is the thickest of the 4 arm nerves on each side. Where they enter the arms the nerves swell but do not assume the form of a string of pearls. The nerves are covered their whole length through the arms with a layer of ganglion cells and are connected at the base by a simple circular commissure; only the nerve of the tentacles is connected with the commissure by short, double branches.

The structural characteristics of the arm nerves stem from their unusual length—due to the neck-like elongation of the head—from the fact that the nerve of the tentacles branches from the 4th arm nerve and, finally, from the formation of a simple ring commissure at the base of the arms.

Earlier authors always stated that there are 5 separate nerves on each side; the fact that the nerve of the tentacles has a common stem with the nerve of the 4th arms is not mentioned. HANCOCK (p. 2) stated that there are 5 further nerves below the bridge commissure, on each side, which later become united with 5 arm nerves that extend from the ganglion brachiale. This is apparently a confusion with the arteries which accompany the nerves; POSSELT (1891, p. 327), describes the condition in *Todarodes* similarly, probably for the same reason. As I do not understand the Danish text, I refer in this respect to the data published by APPELLÖF (1890, p. 8). Unfortunately, this mistake found its way also into later works, e.g. the description of the arm nerves by HESCHELER in LANG's Textbook of Comparative Anatomy (1900, p. 231).

As to the ring nerve at the base of the arms, HANCOCK illustrated a double commissure of the arm nerves in *Ommatostrephes*. APPELLÖF (p. 9, Plate II, Figure 8) found in *Chaunoteuthis* a looped duplication of the commissure which extends free over the arm nerve. I observed such a condition only in the nerve of the tentacles, where however it was not a loop extending over the nerve but two short branches which extend from the tentacle nerve to the ring nerve.

274 **13. Nervi antorbitales superiores.** These nerves (Figures 4, 5, *n. a. o. s.*) extend to the dorsal surface of the orbit. They form 3 or 4 cords on each side from the dorsal surface of the ganglion brachiale to the anterior dorsal musculature of the pillars. These nerves are distinctly visible on each side of the supraesophageal ganglion if the eye is removed from the orbit.

HANCOCK (p. 2) observed these nerves and described two on each side, but without giving details of their course.

14. Nervi antorbitales inferiores. These are two nerves (Figures 4, 5, *n. a. o. i.*) which extend from the lateral ventral margin of the ganglion brachiale to the muscles of the anterior ventral pillars. The posterior nerve is thicker and divides into several branches. I found in one specimen that both stems are united in a loop below the arteria brachialis.

These nerves were not mentioned by earlier authors.

NERVES OF THE SUPRAESOPHAGEAL GANGLION

15. Nervi suprapharyngei. There are two nerves in the large specimen from Station 194 (Figures 1, 5, *n. s. phar.*) which originate on the anterior margin of the supraesophageal ganglion between the commissures to the infraesophageal ganglion. They then branch and innervate the musculature which is situated on the dorsal side of the pharynx. In a slightly younger specimen from Sagami Bay, these nerves are united at the base with the above commissures and branch from them further on.

HANCOCK (p. 4) mentioned and illustrated numerous nerves which extend from the supraesophageal ganglion to the pharynx; no mention is made of them by other authors.

NERVES OF THE INFRAESOPHAGEAL GANGLION

16. Nervi infrapharyngei. In addition to the commissure, two pairs of nerves (Figures 2, 5, *n. i. phar.*) originate on the infraesophageal ganglion—a thicker anterior pair and a thinner lateral pair—which innervate the pharyngeal musculature. There were also two thin separate branches between the anterior pair in one specimen. Hancock observed these nerves, too; he also described an unpaired median branch which extends to the tongue.

17. Nervus sympathicus ("oesophageal nerves" of Hancock**).** The sympathetic nerves (Figures 1, 2, *n. symp.*) originate on the posterior margin of the infraesophageal ganglion as two thin separate stems situated between the commissures. They continue on the esophagus, sometimes covered by connective tissue and neighboring organs, so that they are almost unrecognizable, and extend to the large
275 ganglion gastricum (*g. gastr.*). The ganglion gastricum (Plate XLI, Figure 6; Plate XLII, Figure 3) is rounded and situated on the right side between the opening of the esophagus and the exit of the mid-intestine. It projects slightly beyond the sinus of the stomach and has several branches to the neighboring parts of the intestinal tract. There are two large branches which extend posteriorly; the dorsal stem (Figure 6, *r. stom.*) branches and innervates the musculature of the stomach, while the thick ventral branch (*r. stom. coec.*) extends to the caecum and has a thin branch at the base (*r. pancr.*) to the pancreas. A thicker ventral branch extends anteriorly (*r. d. hep.*) to the ductus hepaticus, and close to it extends a thin nerve to the mid-intestine (*r.*).

Hancock's illustration of the nerves extending from the ganglion gastricum presents on the whole a similar situation; he also states that a commissure extends to the ganglion viscerale—a statement I could not confirm.

Intestinal Tract

The pharynx (Plate XLIII, Figure 4, *phar.*) is moderately large: in a large specimen it is 19 mm long, including the margin of the lips, and 12–13 mm wide. It extends anteriorly from the buccal funnel (*m. bucc.*), which adheres to it by its 7 lamellae of attachment, and is as long as the pharynx, 20 mm from base to the end of the pillars. The esophagus (*oes.*) opens in the pharynx with a funnel-shaped widening above the infraesophageal ganglion and then narrows to a tube which is about 1.5 mm wide and 60 mm long. In two specimens the esophagus forms a diverticulum at about the level of the ganglion viscerale (Plate XLI, Figure 5, *div. oes.*). This diverticulum was stalked and crescent-shaped in one case and formed a spherical vesicle in the other specimen. The esophagus opens in the form of a funnel into a sinus into which open the stomach and caecum and from which begins the mid-intestine.

The **stomach** (Plate XLII, Figures 2–4; Plate XLIII, Figure 1, *st.*) consists of two distinct parts, an anterior muscular stomach and a thin-walled end sac. The large, shining muscular stomach (Plate XLII, Figures 2–4, *st.*) is lined with a thick, light cuticle which projects into the lumen with about 16 longitudinal folds. These folds are best developed in the right and left half of the stomach but disappear gradually toward the thin-walled end sac which has no folds; the end sac was bent in two specimens (Figures 2, 3, *st.'*), and in a third specimen it extended in line with the anterior muscular part (Figure 1).

The **caecum** (*st. coec.*) is well developed but only half as long as the stomach. Its anterior end bears a spiral inflation which is visible already from the outside. From this inflation extend numerous dense folds through the entire anterior part of the caecum. Two swellings pass from the anterodorsally

situated opening of the ductus hepato-pancreaticus to the center of the spiral. The caecum also has a thin-walled posterior part without folds, which appears like a blind sac (Figure 2) in two specimens but is barely indicated in a third.

276 The **mid-intestine** (*int.*) begins in the common sinus anterior to the opening of the caecum and extends ventrally between the two hepatic ducts. It then curves in the form of a horseshoe behind the tip of the liver (Plate XLIII, Figure 1) and continues anteriorly on the ink sac between the two luminous organs. The mid-intestine is not sharply differentiated from the rectum (*rect.*), which opens between the anal lips, slightly anterior to the ventral margin of the funnel. The anal appendages are relatively small (Plate XL, Figure 7; Plate XLII, Figure 1).

Salivary glands. The posterior salivary gland of *Chiroteuthis* is single (Plate XLI, Figure 5). Opening of the animal from the dorsal side (Plate XLIII, Figure 3, *saliv.post.*) shows it to be a compact gland, about 10 mm wide and 9 mm long, situated behind the cranial capsule. In its dorsal groove pass the esophagus, the aorta and the large pallial nerves.

The salivary duct begins as a single tube from the deeply indented anterior margin of the gland, passes through the brain and continues anteriorly on the right side near the esophagus (Plate XLI, Figures 4, 5, *d.saliv.*) before opening in the pharynx, dorsal to the infraesophageal ganglion, at about two thirds of the length of the pharynx. The anterior salivary glands (Plate XLI, Figure 2, *saliv.a.*) are situated on the widened anterior part of the esophagus, near the infraesophageal ganglion. They are small, kidney-shaped and completely separated from each other, at least in their visible parts.

The **liver** (Plate XLII, Figures 2–4, *hep.*) is steeply oriented, corresponding to the elongate structure of the whole body. It is spindle-shaped or, rather, ovoid, because its anterior end is slightly more rounded than the posterior one. The anterior end of the liver is situated at the level of the branching of the visceral nerve, in about the middle of the funnel organ. In a medium-sized specimen, the liver was 24 mm long and 13 mm wide dorsoventrally. The funnel depressors, which converge obliquely anteriorly, are attached at its lateral ventral surfaces.

The hepatic ducts (*d.hep.*) extend upward from the ventral side of the liver to the level of the posterior margin of the ink sac a short way prior to the posterior end of the liver. They are short and thick and have about two large bluntly triangular pancreatic lobes (*pancr.*) on each side. The anterior pancreatic lobes are slightly larger than the posterior ones and are 8 mm long. The end section of the posterior lobes encompasses the hepatic ducts, which in turn encircle the mid-intestine and open in a common opening in the caecum, close behind the mid-intestine (Plate XLII, Figure 4, *d.hep.pancr.*).

The **ink sac** (*atr.*) is best compared to a "Gosen flask". Since such a flask is hardly known outside Saxony, it may be stated that the ink sac has a long, thin anterior part and a strongly widened posterior end which is sometimes heart-shaped indented. The large ventral luminous organs are situated entirely on the broad lateral parts of the ink sac.

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Vascular System

Though I did not examine the vascular system of *Chiroteuthis* as thoroughly as the nervous system, a description of the distribution of vessels as found by examination of the systems of organs would seem to be in order.

Arterial circulation. The **heart** (Plate XLI, Figure 7, *c.*) is situated slightly on the right side behind the dorsal apex of the liver at the level of the base of the gills. Opening of the mantle cavity from the ventral side does not show the heart, which is completely covered anteriorly by the right pancreas

and ventrally by the venous appendages. The heart is more or less spindle-shaped in younger specimens but has a more rhomboidal form in older specimens because it is produced slightly toward the entrance of the branchial veins. The longitudinal axis of the heart is slightly oblique to the median plane of the body.

The aorta cephalica (*a. ceph.*) is dilated, spindle-shaped at the base and ascends obliquely to the right toward the dorsal side of the liver. It branches at first into the arteria pancreatica (*a. pancr.*), which splits into a number of branches to the various lobes.

Further on there originates the thick arteria hepatica, and still further the arteria stellata, which supplies the ganglia stellata (Figure 3, *a.*). On the neck and head the aorta is situated dorsally on the esophagus and is almost as thick as the two pallial nerves (Plate XLIII, Figures 3, 4, *a. ceph.*). The aorta divides into two thick arms at its entrance into the cranium (Figure 4) where it sends off two short branches to the posterior salivary gland (Plate XLI, Figure 5, *a. saliv.*). The two main arms of the aorta again divide into two major inner branches which enter the brain, and two lateral branches, the arteria ophthalmica (Figure 5, *a. ophth.*), which accompany the nervus ophthalmicus superior. They are visible if the roof of the cranial cartilage is removed (Plate XLIII, Figure 4). Anterior to the second bifurcation extend thinner vessels which branch on the posterior part of the cranium. The double bifurcation was symmetrical in one specimen, slightly asymmetrical in another. Before entering the brain between the ganglion viscerale and the ganglion pedale, the inner major branches of the aorta give off a small branch to the nervus opticus.

I have not studied the course of the major vessels inside the brain and would only say that they bend downward and become then visible as the arteria pharyngea and arteria brachialis.

The arteria pharyngea (Figure 5, *a. phar.*) passes through the brain on the right side near the esophagus and extends to the pharynx; here it branches dichotomously below the infraesophageal ganglion and forms 4 branches which supply the pharynx (Figure 2, *a. phar.*).

The arteria brachialis (Figure 5, *a. brach.*) becomes visible ventrally between the ganglion pedale and the ganglion viscerale and then extends anteriorly in the median plane below the ganglion brachiale; it divides into two major branches at about the level of the infraesophageal ganglion which extend anteriorly between the nerve of the tentacles and the nerve to the 4th arms. Behind the ring nerve at the base of the arms, each of these major vessels divides into 3 branches, 2 of which enter the 4th arm and the tentacle, while the third branch accompanies the ring nerve and sends off branches to the 3rd, 2nd and 1st arms.

278 The arteria posterior (Plate XLI, Figure 7, *a. post.*) is not swollen like a spindle at its exit from the heart. It passes behind the renal sacs to the ventral surface of the abdominal wall and has a thick branch near its exit from the heart, the arteria anterior, which extends anteriorly, with lateral branches to the walls of the renal sacs, and later with branches to the ink sac and rectum. From these vessels extend also branches which enter the large ventral luminous organs on the ink sac and divide there into capillaries (Plate XL, Figure 7).

Anterior to the above furcation extends a vessel which apparently represents the arteria genitalis, supplying the gonoducts which, in the specimen examined, were as yet little developed. The main stem of the arteria posterior extends posteriorly in the median line of the abdominal wall and bifurcates behind the gelatinous swelling which enters the cone of the gladius (Plate XLI, Figure 15, *a. pinn.*); the two branches turn dorsally and continue as fin arteries which supply arterial blood to the fin musculature.

Venous circulation. I did not examine the venous circulation in the anterior part of the body very thoroughly, and this goes in particular for that in the arms. The vena cava arises in the head below

the esophagus and can be followed to the brain between the supraesophageal ganglion and the ganglion pedale. It leaves the brain between the exit of the funnel nerves and passes through the base of the cranium between the static organs (Plate XLIII, Figure 2). Immediately behind the cranium is the blind sac of the vena cava (Plate XLI, Figures 5, 9, *coec. v. c.*), which is almost always filled with coagulated blood. It is situated in a pit (Figure 9) which contains large branched chromatophores and borders anteriorly on the ventral musculature of the head, ventrally on the funnel adductors and posteriorly on the cranial cartilage. Since the pit is filled with gelatinous cutaneous tissue, it is visible indistinctly on the lower side of the head, where the blind sac with its whitish coagulated blood is sometimes visible shining through. The vena cava widens after leaving the cranium, curves toward the ventral side of the neck and receives the vena salivalis (Figure 5, *v. saliv.*) from the lower side of the salivary glands. Close behind this point, two veins (*v. cr.*) open symmetrically into the vena cava and ascend along the posterior wall of the cranium, where they enter the cranium at about the level of the salivary glands and widen into sacs behind the ganglion viscerale.

The vena cava extends posteriorly and ventrally and becomes visible on the abdominal wall behind the heart-shaped indentation of the median funnel organ. The vena cava, accompanied by the branches of the nervus visceralis, then curves to the right near the rectum and mid-intestine around the ink sac and the corresponding luminous organ (Plate XLII, Figure 3, *v. c.*). Close to the anus and directly before the bifurcation of the nervus visceralis, the vena cava receives two thin branches which collect venous blood from the ventral luminous organs, depart from the anterior inner margin of the luminous organs, and pass near the branches of the nervus visceralis.

In the area of the renal sac, the vena cava is encumbered with venous diverticula. In older specimens these diverticula form a dense, compact mass which completely fills the whole middle part of the mantle complex behind the ink sac and the mid-intestine. In younger specimens (Plate XL, Figure 7), the
279 mass of diverticula consists of two halves, which are indistinctly divided into a larger anterior and a smaller posterior part. The latter receives on each side the large vena abdominalis (Plate XLIII, Figure 1, *v. abd.*). Along the abdominal wall the abdominal veins collect numerous smaller vessels from the septa situated between the pocket-like spaces of the abdominal wall; they then continue to the beginning of the cone, where they receive small veins from the pallial nerves, and finally extend dorsally and posteriorly.

The complex of venous diverticula receives, in addition to the pallial veins, also veins from the branchial gland (Plate XLI, *v. lien.*), which enter it immediately before the branchial heart.

The **branchial hearts** adhere closely to the venous diverticula. They are visible in their full extent from the dorsal side (Figure 7) as oval or bluntly triangular formations situated close together (*c. branch.*); the relatively small appendages (*app. c.*) of the branchial hearts are situated on their median margin. Short, wide branchial arteries (*a. branch.*) extend from the branchial hearts and pass along the posterior margin of the gills. The branchial veins and their afferent vessels are distinctly visible on the anterior margin of the gill, due to their whitish coloration. The branchial veins widen from the base of the gills into large, thin-walled atria (*v. branch.*) which open into the heart.

As in all Oegopsida, there is a large **renal sac** which is not divided by a median septum. The renal sac is about 15 mm long and wide. It is bordered anteriorly by the luminous organs, laterally by the base of the gills and branchial hearts; its posterior margin forms a curve at about the level of the base of the gills (Plate XL, Figure 7). The loop of the mid-intestine and the nidamental glands are situated on the posterior margin of the renal sac. Dorsally the renal sac is in contact with the heart and its atria, the branchial hearts and the efferent ducts of the genital organs.

The outer openings (*ur.*) are situated behind the luminous organs. They are raised and chimney-

like in some specimens; in others, they form a low papilla, but this may be due to contraction. The inner openings, too, are visible on the ventral side of the renal sac, close behind the outer openings; they widen in the form of a trumpet toward the body cavity.

Genital Organs

I have not examined a single fully mature specimen. The development of the genitalia apparently lags behind that of the body, so that the gonoducts are barely visible. In a male with a gladius of 150 mm length, the testis is only 7 mm long. The testis is situated on the dorsal wall of the stomach at the point wmere the gastrogenital ligament begins (Plate XLI, Figure 20). The testis (*test.*) adheres closely to the ligament and surrounds it like wings (Figure 19). During further growth, the lateral wings of the testis extend ventrally, surround the sides of the stomach and become contiguous behind it in the median plane. I found such a condition of the ovary in the large female from Station 194 (Plate XLIII, Figure 1, *ov.*) in which a ventral slit forms the boundary between the back-folded wings. As the genital gland
280 grows, so the gastrogenital ligament lengthens and moves increasingly deeper, as already mentioned (see p. 203), ending in the gelatinous mass inside the cone of the gladius.

The gonoducts show conditions normal for the Oegopsida; they are bilateral in the female and unilateral, i.e. situated on the left side, in the male. Since my specimens were immature, their gonoducts were little developed.

I made a preparation of the gonoducts of a medium-sized male (Plate XLI, Figures 17, 18). They are 16 mm long and are situated on the left side between the branchial heart and the anterior part of the stomach and caecum. The opening (Figure 17, *amp.*) of the vas deferens is visible only upon examination from the dorsal side. It lies posteriorly and is of slit-like form. The vas deferens is only slightly undulate and passes anteriorly into the first glandular part of the vesicula seminalis (*ves. sem.*^{1}). The latter leads into the second or middle part (*ves. sem.*^{2}), from which it is sharply differentiated. The 2nd and 3rd (*ves. sem.*^{3}) parts of the vesicula seminalis are visible from the ventral side their whole length. Near its opening into the vas efferens (Figure 17, *v. eff.*), which, too, is visible only from the dorsal side, the caecum and the long glandular sac of the prostate (*app. post.*) are situated. The vas efferens opens in the posterior quarter of the spermatophore pocket (*b. sperm.*) which is still little developed and forms a slightly *S*-curved duct with a widened, spatulate outer opening (*pen.*) behind the base of the gills.

The oviducts were also in an early stage of development, although it was precisely the larger specimens that proved to be females. Those of younger females were not visible at all from the outside, as they were completely covered behind the branchial hearts. The oviducts (Figure 7, *od.*) became visible in their whole length only during examination of the mantle complex from the dorsal side. The oviducts are situated obliquely to the longitudinal axis of the body and already show the characteristic division into an undulate posterior duct, a straight middle part, and the oviduct gland, which is situated around the opening. The oviduct gland surrounds the slit-like, ventrally situated openings (Figure 8) and swells behind them into an oval pad. The largest specimen had an oviduct 17 mm long but fitted otherwise readily into the stage described here. Its openings are slightly protruding dorsal to the base of the gills. The oviduct then passes obliquely on the dorsal surface of the renal sac to the posterior wall of the renal sac and ends near the point where the arteria posterior appears on the external abdominal wall. I made a preparation of the right oviduct, which showed a slight anomaly: one of the lips which border the slit-like opening was slightly gelatinously swollen, but the glandular lamellae which extended obliquely to the opening were distinctly visible. The posterior part of the oviduct gland forms a circular

swelling and bears a system of folds which is visible from the outside. Then follows the longer, straight part of the oviduct, and finally the initial part, which forms numerous narrow loops. A skin fold which
281 surrounds the opening and lips of the oviduct gland and forms a "peritoneal sinus" was visible already in the youngest specimen (Figure 8). As mentioned in the description of the nervous system, branches of the branchial nerve supply the oviduct and oviduct gland.

Sexual maturity thus develops apparently very late in *Ch. imperator.* These proud forms must be reaching a gigantic size before they become sexually mature. This may explain that not a single specimen of *Chiroteuthis* with hectocotylized arms has been described. Careful examination of the arms of the male showed no indication of hectocotylization. It is questionable whether hectocotylization takes place at all. Verrill (1881, p. 410) described a male of *Ch. lacertosa* which had spermatophores but showed no indication of hectocotylization. Since *Ch. lacertosa* is apparently identical with *Ch. veranyi,* I may add that in a well-preserved male of *Ch. veranyi* at my disposal, I did not find any indication of hectocotylization either.

Measurements of *Chiroteuthis imperator*, Station 194 (near Sumatra)

Dorsal length of mantle to base of fins	78 mm
Length of fins	100 mm
Width of both fins together	86 mm
Posterior end of body	31 mm
Total dorsal length to margin of mantle	209 mm
Dorsal length of head (dorsal corner of mantle to base of arms)	63 mm
Ventral length of head	69 mm
Left dorsal arm	101 mm
Left 2nd arm	126 mm
Left 3rd arm	156 mm
Left 4th arm	207 mm
Length of tentacle club	118 mm

Chiroteuthis veranyi Férussac, 1834

(Plate XL, Figure 1; Plate XLII, Figure 5; Plate XLIV, Figures 1, 2, 4, 5)

This magnificent form has been repeatedly described, but a new description seems indicated, with particular emphasis on the differences between the species and the subgenus *Chirothauma.* I would like to mention some points which concern either new data or structural conditions that have not been adequately described. The following description is based on two well-preserved specimens from Messina, male and female, which are preserved completely intact in formol. I am indebted for them to Cialona, who collected rare deep-sea forms which occasionally appear at the surface in the port of Messina.
282 Comparison of the sizes of the two subgenera shows that the ventral arms of *Ch. veranyi* are longer than the body, those of *Chirothauma* barely as long as the body. The male of *Ch. veranyi* is 130 mm long from the base of the ventral arms to the tip of the body, and its ventral arms are 185 mm long. Unlike *Chirothauma* (cf. p. 192), *Ch. veranyi* is thus characterized by its (relatively to the body) large arm apparatus.

As regards other differences, *Ch. veranyi* has a goblet-shaped mantle with a not very markedly projecting dorsal corner. The mantle tapers to a slender gelatinous stalk in the area of the fins and ends

at the level of the posterior margin of the circular disc formed by the fins. On the other hand, the spindle-shaped posterior end of the body of *Chirothauma* projects beyond the fins and bears a thin accessory membrane. This is the most important difference between the two subgenera.

Other important differences are to be found in the physiognomy of the head. The head of *Ch. veranyi* is bolt-shaped, relatively short, and wider than the mantle because of the very large eyes—each of which is 24 mm wide, i.e. nearly as large as the visceral sac (Plate XL, Figure 1). The renal papilla is situated 21 mm from the apex of the stomach, which is less than the width of the eye. The same part in *Chirothauma* is at least twice as large as the width of the eye. There is a distinct sinus on the eye in only one specimen; the sinus disappears completely if the lid fold is extended, which may explain earlier statements that it is absent. The development of a thick pad of circular fibers causes here, too, a crescent-shaped thickening of the posterior margin of the lid fold.

The olfactory tubercles are distinct behind the eyes; their stalks are 3–4 mm long and they are therefore the longest of all Cephalopoda.

The arms become gradually larger in the dorsoventral direction; they are keeled their whole length by swimming membranes. The latter become gradually wider from the dorsal to the ventral arms; they are situated lateroventrally on the first 3 pairs of arms, laterodorsally on the ventral arms. If the arms are held together, the ventral swimming membranes, which are 14 mm wide, cover the 3rd arms completely and part of the 2nd arms.

Chirothauma shows no striking difference in the arrangement of the suckers on the 4th arms, while in *Ch. veranyi* these suckers are much more loosely arranged, and the suckers of the dorsal row alternate, though not strictly, with the adjacent luminous organs, of which there are 24 on the right and 19 on the left ventral arm of the adult male.

283 The data on the protective membranes are rather vague and it should be noted that they are well developed on all arms; they were probably overlooked because their muscular supports coincide with the proximal margin of the conical widenings of the stalks of the suckers.

The **tentacles** show no distinct structural differences between the two subgenera. But the stalks of the suckers of the tentacles of *Ch. veranyi* bear a thickened ring of black stripes of pigment, as already illustrated by Férussac and d'Orbigny. The glandular knobs on the dorsal side of the tentacle stalk resemble those of *Chirothauma,* and so does the 3 mm long finger-shaped glandular knob at the tip of the club. The protective membranes of the club extend for some distance on the lateral surfaces of the glandular knob and its slit-like 2 mm long opening is situated on the outer side and is surrounded by a brownish black skin fold.

I did not find any indication of hectocotylization in our species. One of the large specimens is a male (though not fully mature), but its arms do not differ in any character from those of a female of about the same size. Nor did Verrill, who described this species as *Ch. lacertosa.* He stated explicitly that his specimen was fully mature and had numerous spermatophores in Needham's sac but showed no sign of hectocotylization.

Ch. veranyi does not have the bright reddish **coloration** of *Chirothauma.* According to Vérany, the live *Ch. veranyi* is paler and more transparent but shows a number of characteristic shining stripes and spots which are luminous organs and which were described above (p. 197). There is an important difference in the arrangement of the luminous organs: *Chirothauma* has 3 rows of lens-shaped organs on the ventral side of the eyeball, while the organs of *Ch. veranyi* form two long, golden stripes (Figure 1). They are distinct in the preserved specimens; in addition to these stripes, which were already noted by Vérany, there are 3 isolated lens-shaped organs—two at the end of the stripes, i.e. where the two stripes converge into an angle, and the third between the two sides of this angle.

Inner organization
(Plate XLII, Figure 5)

The mantle complex of *Ch. veranyi* has been described by Weiss (1889), who also gave a generally correct description of the conditions in the young specimen he examined. However, Weiss made a few serious errors in the interpretation, which I will correct, adding a number of details.

Opening of the mantle from the ventral side shows that the very delicate septum, which was not men-
284 tioned by Weiss, is displaced far posteriorly. The posterior margin of the funnel is straight and situated a short distance anterior to the anus; the funnel depressor (*mu. depr. inf.*) is therefore visible almost its whole length in the form of a fan which widens from the base of the gills toward the anus and ends in the dorsal wall of the funnel. On the median side of the large liver extend the mid-intestine and the rectum which forms a thick swelling and bears relatively small anal appendages. Below the rectum is the ink sac (*atr.*), the posterior part of which is heart-shaped and serves as a pigmented envelope for the ventral luminous organs (*luc.*). As mentioned above (p. 197), Vérany (p. 120) described them as a "gross point à reflect métallique argenté." Strangely enough, Weiss regarded them as accessory nidamental glands.

Around the right organ passes the vena cava, which forms a wide curve before entering into the large renal sacs. The renal sacs are completely surrounded by the venous appendages (*sacc. v.*), which are compact and have an only indistinctly divided posterior part. The projecting chimney-like outer openings of the renal sacs are situated laterally behind the organs. The venous appendages receive posteriorly the large venae abdominales (*v. abd.*), which are filled with whitish coagulated blood. The oval branchial hearts (*c. branch.*) are situated on the sides of the renal sacs and a relatively long branchial artery extends from them to the dorsal part of the gill. The gills of the large male are 12 mm long. They are of pyramidal form with 20 lamellae on each side and, as in all Oegopsida, the outer lamellae are much longer than the inner ones. The branchial ligament (*susp. branch.*) is strong and slightly longer than in *Chirothauma.* On the ventral crest of the gill passes the branchial vein, which widens markedly toward the base of the gills and then passes into the thin-walled atria. The arteria posterior (*a. post.*), which passes on the median line of the abdominal wall, is more delicate than in *Chirothauma.* The stomach (*st.*) is large and ovoid. The caecum (*st. coec.*) is much smaller; it has a spiral swelling with radial folds near the gills and posteriorly a process like a caecum which is differentiated from the spiral swelling. The stomach is also suspended on the long gastrogenital ligament (*lig. g. g.*) which widens posteriorly and becomes gelatinous; as in *Chirothauma*, the gastrogenital ligament ends in a slightly swollen gelatinous pad which enters into the sinus. The stomach is bordered laterally by the thick pallial nerves (*n. pall.*), which extend toward the fins. On the dorsal side of the stomach of the male there is the broad, thin testis (*test.*), which is 7 mm long. The testis forms an undulating band which extends from the caecum to about the middle of the stomach, where it is situated on the gastrogenital ligament. The male gonoducts resemble those of *Chirothauma.* They are not yet fully developed in the male examined and are situated on the stomach and caecum behind
285 the branchial heart. Their spatulate opening (*pen.*), which is situated dorsal to the base of the left gill, and the sickle-shaped spermatophore sac (*b. sperm.*), which surrounds the left renal sac, can be seen from the outside. The ovary of a female projects slightly posteriorly beyond the stomach. It consists of two lobes which perhaps extend to the ventral side of the stomach in the mature animal. It is hard to understand why Weiss (Plate 8, Figure 7) placed the whole ovary of a younger specimen on the ventral side of the stomach. My specimen has slightly curved nidamental glands which are situated on the renal sac near the entry of the abdominal veins.

Doratopsis DE ROCHEBRUNE 1884

Loligopsis vermicolaris RÜPPELL, 1844, *Cefalop. di Messina*, Lettera al Prof. Cocco.
Loligopsis vermicolaris GRAY, 1849, *Cephalop. Antepedia*, p. 40.
Loligopsis vermicularis VÉRANY, 1851, *Céphalop. Médit.*, p. 123, Plate 40, Figures a, b.
Doratopsis vermicularis, D. rüppelli, 1884, DE ROCHEBRUNE, *Loligopsidae*, pp. 12, 13.
Hyaloteuthis vermicularis 1884, PFEFFER, *Ceph. Hamb. Mus.*, pp. 22, 28, Plate III, Figure 30.
Leptoteuthis diaphana 1884, VERRILL, *Moll. New Engl.*, pp. 140, 141, Plate XXXII, Figure 1.
Doratopsis vermicularis 1884, HOYLE, *Loligopsis*, p. 329.
Doratopsis vermicularis 1886, HOYLE, *Rep. Challenger*, p. 43.
Doratopsis vermicularis 1889, WEISS, *Oig. Cuttle Fishes*, p. 80, Plate IX, Figures 1–9.
Doratopsis vermicularis 1896, JATTA, *Cefalopodi Nap.*, p. 108, Plate VII, Figure 22; Plate XIV, Figures 1–9.
Doratopsis vermicularis 1899, FICALBI, *Chiroteuthis e Doratopsis*, pp. 93–118, Plate I.
Doratopsis vermicularis 1900, PFEFFER, *Syn. Oeg. Ceph.*, p. 186.
Doratopsis vermicularis 1903, JATTA, *Alc. Cefalop. Medit.*, pp. 193–198.
Doratopsis vermicularis 1904, HOYLE, *Gen. Rec. Dibr. Ceph.*, pp. 16, 20.
Doratopsis sagitta, D. exophthalmica, D. lippula 1908, CHUN, *Ceph. Deut. Tiefsee-Exp.*, p. 89.
Doratopsis vermicularis 1909, MASSY, *Ceph. Dibr. Ireland*, p. 33.
Doratopsis vermicularis, D. sagitta, D. exophthalmica, D. lippula 1909, HOYLE, *Catal. Rec. Ceph.*, II, *Suppl.*, pp. 274, 275.

The expedition collected 6 specimens of a delicate transparent, arrow-shaped form of Chiroteuthidae which show the characteristic form of the genus *Doratopsis*. Closer examination showed that the specimens differ markedly from the Mediterranean species *D. vermicularis* and belong to 3 groups of forms. Whether they are 3 distinct species or are juvenile forms of Chiroteuthidae will be discussed below.

E. FICALBI (1899) considered the genus *Doratopsis* to be the larval form of *Chiroteuthis*. As this view was confuted by two renowned specialists, PFEFFER and HOYLE, it seems advisable to recapitulate the discovery of these forms and follow it up with a critical discussion of their generic characters. I will describe the specific differences of the forms and give some data on their hitherto incompletely known inner organization, with particular reference to the genital conditions. We will then examine the question whether the genus is valid or represents a juvenile form of *Chiroteuthis*.

286 The history of discovery of these forms will be summarized only briefly, since a detailed historical description has already been published by JATTA and FICALBI. This striking and rarely observed form was first collected in 1844 in Messina by E. RÜPPELL, who placed it in the genus *Loligopsis*, as species *L. vermicularis*. VÉRANY (1851) described and illustrated it under this name in his comprehensive honograph "*Céphalopodes de la Méditerranée*."

This species retained the generic name of *Loligopsis* for 40 years. By coincidence, 3 authors removed this species from *Loligopsis* in the same year, 1884, and established 3 new genera for it.

In his work on the Cephalopoda of the Museum of Hamburg, PFEFFER (1884) pointed out that very heterogeneous forms were included in *Loligopsis* and created the new genus *Hyaloteuthis* for this form.

In the same year (1884), VERRILL described a form as *Leptoteuthis diaphana* and stressed its close relationship to *L. vermicularis*. He placed *D. diaphana* and *D. vermicularis* in the genus *Leptoteuthis*.

In his monograph on the Loligopsidae, DE ROCHEBRUNE suggested that *Loligopsis* be divided into several genera. He established the genus *Doratopsis* for *L. vermicularis* and divided the species *vermicularis* into two species, *D. vermicularis* and *D. rüppelli*, because of minor differences between them in VERANY's illustrations.

Of the names *Hyaloteuthis*, *Leptoteuthis* and *Doratopsis*, only the last can be maintained, because the other two are preoccupied. Thus it is the name *Doratopsis* that is used in later publications, i.e. in the *Challenger Report* by Hoyle (1886), by Weiss (1899), and in the monograph of Jatta (1896). Pfeffer (1900) considers the Mediterranean form to be identical with Verrill's *Leptoteuthis diaphana*, while Hoyle considers it to be a different species.

To date there are thus one, respectively two, species of *Doratopsis* known. Of these, the Mediterranean *D. vermicularis* has been described in detail by Pfeffer, Weiss, Jatta and Ficalbi, who restricted themselves, however, to its external characters. Whether *Leptoteuthis diaphana* differs specifically from the Mediterranean form is hard to decide from Verrill's description and illustration. Not described by Verrill are the very characters which, due to their importance, I intend to use for the distinction of these forms: the presence of a keel on the tentacle club and the position of the olfactory tubercles. All one can therefore say, for the time being, is that Verrill's specimen appears to be an older animal in which the ventral arms already bear luminous organs. Otherwise his form more or less agrees with older specimens of *D. vermicularis*.

Summarizing the characters considered by the various authors to be characteristic for the genus *Doratopsis*, I would start by giving the diagnosis of Pfeffer (1900, pp. 184, 186), which, cited in abbreviation, is as follows:

287 "Locking cartilage of funnel with tragus and atitragus; a longitudinal ridge in the cartilaginous pit. End of mantle and gladius projecting beyond posterior margin of fin. Club with distinct swimming membrane; suction organ of tip of tentacle rudimentary, without opening on the dorsal side of the club, and without large median tooth on the high side of the suckers of the tentacles."

Pfeffer's diagnosis needs a critical revision, because the 6 specimens collected by the German Deep-Sea Expedition in the Atlantic and Indian oceans belong to at least 3 species which differ distinctly from *D. vermicularis*. Although the new forms of *Doratopsis* were at Pfeffer's disposal, he did not even consider placement of these species in the latter genus.

As regards the form of the funnel and mantle cartilages, in a specimen of *D. vermicularis* from Messina at my disposal (Plate XLVII, Figure 3), I looked in vain for the longitudinal ridge in the pit of the funnel cartilage mentioned by Pfeffer; nor did I find the opposite part of this ridge, namely a groove, on the noselike mantle cartilage. Only the insertion of the bandlike funnel depressor is visible through the pit of the funnel cartilage, and that could certainly not have been held by Pfeffer to comprise a longitudinal ridge. This is thus apparently a variable character, not to be used for the diagnosis of a genus. Also to be kept in mind is that the new forms of *Doratopsis* show a striking variation in the form of the funnel cartilage: the funnel cartilage of *D. sagitta* forms a long, flask-shaped pit without tragus or antitragus (Figure 1); the groove of *D. lippula* and *D. exophthalmica* contains an antitragus (Figure 2).

The club is also of varying form. In *D. vermicularis* there is a distinct swimming membrane in the form of a keel which is displaced to the dorsal side and extends in the tip. *D. sagitta* and *D. lippula* (Plate XXXIX, Figure 12) show a similar condition, but there is no indication of a swimming membrane in the two specimens of *D. exophthalmica* that are at my disposal.

The other characters mentioned, the lack of a "suction organ" (glandular knob) at the tip of the tentacle and the absence of a large median tooth on the high side of the suckers of the tentacles, do not justify separating the genus *Doratopsis* from *Chiroteuthis*. I did not find any dentition on the margin of the suckers of the tentacles in my specimen of *D. vermicularis*, although this is common in juvenile forms. The typical form of suckers, e.g. the transformation into hooks, develops only during postembryonic metamorphosis. The absence of a so-called "suction organ" on the tip of the tentacle can-

not be used for a division into genera either. I found a small, knoblike subapical thickening on the outer side of the club of *D. vermicularis* which may well develop into a glandular knob.

Thus, of all the characters mentioned above, the more important ones are variable, and the minor ones, e.g. the absence of a glandular knob and the absence of a large median tooth, may be due to a juve-
288 nile condition. The only remaining characters of the genus *Doratopsis* are thus the slender body, the long, rodlike gladius and the large ventral arms. Although these characters are not sufficient for a sharp diagnosis of the genus, it seems useful to maintain the name *Doratopsis* for the time being. Examination of the different forms has shown that the following characters are of special importance for the distinction of the species:

1. The position of the olfactory tubercles, which may be situated close behind the eyes, respectively behind the optic ganglia, or far from the eye at the level of the funnel.
2. The form of the eyes. These may be spherical and sessile, or oval and protruding. In the latter case, the eye has a ventral conical or rounded process so that it sometimes has a bizarre form (Plate XLVI, Figures 5, 7).
3. The arrangement of the suckers on the large ventral arms. The suckers may be densely arranged in two distinct rows (Plate XXXIX, Figure 15), or widely spaced and forming a more or less single row (Figure 14).
4. The form of the club, inasmuch as it does or does not have a keel (swimming membrane). Furthermore, the club may be long and not wider than the stalk of the tentacle, or relatively short and markedly widened.

If the above characters are resorted to for a distinctive characterization of *Doratopsis*, the following key will be obtained:

Olfactory tubercle at level of funnel. Eye sessile, spherical. Ventral arms with suckers in 2 rows. Club relatively short, slightly widened, with keeled dorsal side. Funnel cartilage flask-shaped, without tragus or antitragus.
D. sagitta Chun

Olfactory tubercle situated near optic ganglion. Ventral arms with suckers in about one row. Funnel cartilage ear-shaped.

- Eyes not protruding, without ventral processes. Club long, hardly wider than the stalk, with keeled dorsal side. Funnel cartilage with tragus and antitragus.
  D. vermicularis Rüppell (*diaphana* Verrill)
- Eyes protruding, oval, with ventral processes. Funnel cartilage with antitragus.
  - Club without keel, long, not wider than stalk.
    D. exophthalmica Chun
  - Club keeled, short, slightly widened.
    D. lippula Chun

289 ## *Doratopsis sagitta* Chun
(Plate XXXIX, Figure 15; Plate XLV, Figures 1–5; Plate XLVII, Figures 1, 5, 6)

Doratopsis sagitta Chun, 1908, p. 89.

Locality: Station 39: Guinea Current, 14°39′ N, 21°51′ W. Vertical net to 2,500 m—One specimen.
Station 172: South Indian subtropical calm zone, 30°6′ S, 87°50′ E. Vertical net to 1,800 m—One specimen.

I have two specimens of this completely transparent form, a younger and an older one. They were collected in the Atlantic near Cape Verde (Station 39) and in the South Indian subtropical calm waters (Station 172). Both specimens are intact, except the posterior rodlike end of the gladius—always very fragile.

The larger specimen from Station 172 (Plate XLV, Figures 1, 2) is 42 mm long, including the ventral arms. The mantle is scarcely wider than the long neck and narrows between the dorsal base of the fins into a peak which projects only slightly behind the posterior margin of the fins. The fins are relatively large and together 11 mm wide; their dorsal base is 7 mm long. The two fins form together an ellipse. The mantle has a sharp dorsal corner, but its ventral corners are barely indicated. The cylindrical head is 8 mm long. It tapers conically toward the base of the arms. Because of the small, nearly spherical eyes, the head is not markedly widened at the level of the eyes (Plate XLV, Figure 5). The iris has a metallic sheen in the live animal, and the lid has a distinct sinus. Characteristic are the long optic ganglia, which are nearly twice as long as the eyes and are widely separated on the sides of the neck, so that the brain and, at the level of the eyes, the supraesophageal ganglion (Plate XLVII, Figure 6) are distinctly visible.

The olfactory tubercles are situated markedly far from the eyes and from the posterior margin of the optic ganglia which are situated on each side of the funnel. The nervus olfactorius extends superficially to the small tubercles.

The funnel (Plate XLVII, Figure 1) is relatively slender and contains two large, flask-shaped funnel cartilages without tragus or antitragus.

The ventral arms are larger than the other arms; they are 13 mm long in this specimen. The ventral arms bear densely arranged biserial suckers to the tip (Plate XXXIX, Figure 15). The arm formula is 4, 2, 3, 1. The tentacles have a relatively short club with a distinct keel on the dorsal side. The club is only slightly widened and bears numerous irregularly arranged, small suckers in the proximal part, but in its main part there are 4 parallel rows the two ventral rows of which have slightly larger suckers
290 than the dorsal rows. The whole body is covered with small chromatophores and is almost completely transparent in life. A few larger dorsal chromatophores are situated around the eyes.

The smaller specimen, caught in a vertical net at Station 39 in the Guinea Current, shows similar characters (Plate XLV, Figures 3, 4). It is 27 mm long, including the ventral arms, and its dorsal mantle length is 14 mm. A lobe of skin surrounds the end of the gladius, of which only 1 mm is preserved. The combined width of the fins is 7 mm; neck and head are 5 mm long from the dorsal margin of the mantle to the base of the arms, and the ventral arms are 6 mm long. Since this specimen closely resembles the larger one in all the essential characters (Figure 5 shows the head in lateral view), a detailed description is not necessary and I refer to the illustrations.

Doratopsis exophthalmica Chun
(Plate XXXIX, Figures 11, 13, 14; Plate XLVI, Figures 1–5; Plate XLVII, Figure 2)

Doratopsis exophthalmica Chun, 1908, p. 89.

Locality: Station 26: Canaries Current, 31°59′ N, 15°5′ W. Vertical net to 2,500 m—One specimen.
Station 169: South Indian subtropical calm zone, 43°13′ S, 80°30′ E. Vertical net to 2,000 m—One specimen.

I have two specimens of this species. The larger was found east of Madeira (Station 26), the smaller in the South Indian calm zone (Station 169).

The larger specimen (Plate XLVI, Figures 1, 2) is 55 mm long, including the ventral arms, and its dorsal mantle length is 25 mm. The mantle is 30 mm long if the end of the gladius is included, which projects 5 mm beyond the fins. The mantle is relatively wider than in other species of *Doratopsis*; it narrows at the level of the dorsal base of the fins to a point which projects 5 mm beyond the fins and is surrounded by a thin undulate membrane. The fins resemble butterfly wings and have a combined width of 9 mm; their relatively short dorsal base is only 2 mm long. The dorsal corner of the mantle projects distinctly, the ventral corners are barely distinguishable.

The funnel is conical and projects markedly; its oval cartilage has a distinct antitragus but no trace of a tragus (Plate XLVII, Figure 2). The neck is relatively shorter than that of the other species and continues in the very wide head, which is 5.5 mm wide.

The width of the head is caused mainly by the markedly protruding eyes, which end ventrally in a conical process (Plate XLVI, Figure 5). The eyes are oval and have no sinus; immediately dorsal to
291 them there are the large optic ganglia, which are almost contiguous anteriorly and surround the brain with a heart-shaped posterior indentation. The stalked olfactory tubercles are situated immediately behind the eyes. The head is lengthened into a "head pillar" (p. 3) which bears the large arms. The ventral arms with their broad swimming membranes are markedly longer than the other arms; they are 21 mm long and bear 10 nearly uniserial suckers only in the proximal part (Plate XXXIX, Figure 14). The arm formula is 4, 2, 3, 1.

The tentacles are about a third longer than the ventral arms and have a slender club which is scarcely wider than the stalk (Plate XXXIX, Figures 11, 13). The tentacles have narrow protective membranes but there is no trace of a keel-shaped swimming membrane. Their rounded outer surface is yellowish brown. The proximal half of the club of the larger specimen (Figure 13) bears 5 pairs of biserial suckers, then follow rows of 3 and then more numerous rows of 4 suckers. The suckers at the tip are again arranged in biserial rows. The arrangement of the suckers on the club of the younger specimen is similar (Figure 11), but the proximal rows of two suckers are more irregularly arranged and there are no biserial suckers at the tip.

The live animal is vivid yellowish brown, with strongly pigmented chromatophores on the fins, on the ventral and dorsal side of the mantle, on the dorsal side of the neck and on the outer surface of the arms and tentacles. There were also two bright red chromatophores at the anterior, and two black ones at the posterior margin of the eyes. The bright red liver showed distinctly through the mantle.

The smaller specimen from the Indian Ocean (Plate XLVI, Figures 3, 4) closely resembles the above specimen in all important characters. This specimen, the habitus of which is shown in the figures, has a dorsal mantle length of 9.5 mm, including 1.5 mm of the free end of the gladius. The dorsal base of the fins is relatively short (1.5 mm) compared with the combined width of the fins (3.8 mm). Head and neck are 8 mm long to the base of the arms; they form an oblong cone laterally on which the strongly

protruding eyes are situated. The eyes have a very long ventral process (Figure 5). The ventral arms are 7 mm long and in this specimen, too, bear uniserial suckers.

Doratopsis lippula CHUN

(Plate XXXIX, Figure 12; Plate XLV, Figures 6, 7; Plate XLVI, Figures 6, 7).

Doratopsis lippula CHUN, 1908, p. 89.

Locality: Station 74: Benguela Current, 11°28'N, 10°24'E. Vertical net—One specimen.

I have one intact specimen of this delicate form from the Benguela Current (Plate XLV, Figures 6, 7) and the anterior end of another specimen from the same catch (Plate XLVI, Figure 6). Their total length is 24 mm, the dorsal mantle length being 16 mm, including the free end of the gladius which
292 measures 2 mm. The fins have a long dorsal base and are slightly longer than wide. The mantle is of normal form. The funnel projects in the form of a cone and bears a flask-shaped cartilage with only a trace of an antitragus. The head is 8.5 mm long and is inflated by the strongly protruding eyes; the neck is slightly shorter than the head pillar. Especially prominent are the dorsal and ventral longitudinal muscular lamellae which extend at about the level of the brain and the supraesophageal ganglion; the ventral muscles are superficial, the dorsal muscles are situated deeper.

The oblong oval eyes (Plate XLVI, Figure 7) protrude markedly and have a thick ventral process. The optic ganglia resemble those of *D. exophthalmica*; the olfactory tubercles are situated immediately behind them.

The ventral arms are 13 mm long and have more or less uniserial suckers which reach to about the middle of the arms. The swimming membrane is displaced to the laterodorsal margin and there are very thin protective membranes.

D. lippula resembles *D. exophihalmica* in general form but differs distinctly in the form of the tentacle club (Plate XXXIX, Figure 12), which is relatively short, wider than the stalk and bears a markedly projecting keel-shaped laterodorsal swimming membrane. The proximal suckers of the club are arranged in an indistinct biserial pattern, then form 3 rows, and finally pass into the normal arrangement of 4 rows. There is no marked difference in size between the dorsal and ventral suckers of the club, as was the case on the club of *D. sagitta*, which resembled it in shape.

The coloration is less intensive than in *D. exophthalmica*, but there are yellowish brown chromatophores on the mantle, head and arms.

Two other larvae belong without doubt to the developmental cycle of the species of *Doratopsis* described. They are interesting because they are the youngest stages known. The oval form of the eyes and the indication of a ventral swelling suggest that the larvae perhaps belong to *D. lippula*. The characteristic arrangement of the muscular lamellae of the head pillar is also the same. These larvae have stump-shaped ventral arms which in the larger specimen are longer than the other arms, although they are only 1 mm long. The arm formula is 4, 3, 2, 1. The larger larva was caught with a vertical net at Station 215 in the southern part of the Bay of Bengal; it is only 9 mm long, including the tentacles, and has a dorsal mantle length of 5 mm.

The youngest larva is even more interesting (Plate XLVI, Figures 8, 9, 10). Its form shows that it is a larva of *Doratopsis*: the goblet-shaped, relatively broad mantle ends in a point which projects

beyond the small fins, and the head consists of a neck and pillar. This larva is 6.5 mm long, including
293 the ventral arms; the mantle is 4 mm long. The small fins are spatulate and wider than long; their combined width is 3 mm. The neck is relatively slender, but the large optic ganglia cause a marked widening in the middle of the head. The eyes protrude slightly and show an indication of a ventral swelling; the olfactory tubercles are not recognizable. The arm apparatus is markedly retarded. All arms form short stumps of about the same size, only the 3rd arms are slightly shorter, being so tiny that they are barely visible stumps. The 1st, 2nd and 4th arms bear only 3 small suckers each. The arm formula, if it could be determined at all with these short stumps, would be 1, 2, 4, 3.

The tentacles are covered with suckers almost from the base and become gradually smaller toward the tip. There are 4 or 5 large proximal suckers in a more or less uniserial arrangement; the smaller distal suckers are more or less biserial.

This larva was caught at Station 228 in the Indian Countercurrent.

Inner organization

(Plate XLVII)

The inner organization of *Doratopsis* is almost unknown; the brief notes of Weiss (1889, pp. 81, 82, Plate IX) refer mainly to the topography of the organs visible if the mantle cavity is opened and give no information on the genital conditions. As it was important to determine whether the genitalia show larval characters or are developed far enough to justify the establishment of *Doratopsis* as a genus, I give a description of the inner organization of a *D. vermicularis* from Messina and of the larger specimen of *D. sagitta*, as obtained by section.

The **head part** (Figure 6) is illustrated after a preparation of *D. sagitta* cleared in oil of cloves. The almost spherical eyes are widely separated by nearly twice the length of the axis of the eye. The optic ganglia (*g. opt.*) are unusually long; they are situated at the sides of the head and leave between them a wide median space which is filled by the brain (*g. cer.*) and the supraesophageal ganglion (*g. bucc. sup.*). Behind the brain is the fanlike salivary gland (*saliv.*), which covers the large static organs. Because of the black staining with osmic acid, the vessels and nerves along the esophagus (*oes.*) are not distinctly visible, but they are distinct in *D. vermicularis*, in which the aorta cephalica passes on the right, near the esophagus, and the two broad bands of the nervus pallialis extend to the outer side. The large mantle ganglia are situated close together in the anterior part of the mantle. The thick fin nerves extend from these ganglia, as a posterior continuation of the mantle nerves, and pass close
294 together in the dorsal midline of the body (Figure 3, *n. pall.*).

The head of *D. vermicularis* differs from that of *D. sagitta* in its relatively larger eyes which leave between them only a narrow median space, about half as wide as an eye. The optic ganglia are almost fused anteriorly; posteriorly they surround the brain and closely adhere to it. A similar condition obtains in *D. lippula* and *D. exophthalmica.*

The neck of all forms of *Doratopsis* is very long, gelatinous and pervaded by muscular septa. The septa of *D. sagitta* are not as regularly arranged as in *D. vermicularis*, in which they were observed by earlier authors. Weiss mentions 8 septa, Jatta only seven. There are 8 septa in my specimen, the posterior one directly above the collaris. Similar septa are situated in the head pillar, where they have a more honeycomb-like arrangement and are more densely arranged between the eyes.

Weiss (1889, p. 81) noted peculiar stellate organs in the dorsal part of the neck of *Doratopsis*. I did not find these organs so regularly arranged as described by Weiss; I consider them as juvenile

chromatophores with muscular processes but still without pigment. JOUBIN (1900), too, found chromatophores at these points in a specimen of *D. vermicularis* and assumed that these may be the stellate organs of WEISS.

Funnel. The funnel adductors (Figure 3, *mu. add. inf.*) are the continuation of two long, bandlike muscles which pass on the ventral side of the neck. These wide bands pass at the sides of the vena cava (*v. c.*) and branch prior to the funnel into an adductor anterior and posterior. They can be followed anteriorly to the level of the brain. They correspond to the large adductors of *Chiroteuthis* (p. 190).

Opening of the mantle cavity of *Doratopsis* (Figure 3) shows the oval ventral parts of the funnel organ (*org. inf.*). Also visible are the bandlike funnel depressors (*mu. depr. inf.*), which are situated on the liver and closely resemble those in *Chiroteuthis*. The anterior base of these muscles is visible through the funnel cartilage, which has a well-developed tragus and antitragus in *D. vermicularis*.

Intestinal tract. The esophagus opens dorsally below the liver into a part of the stomach which is very long in *D. sagitta* (Figure 5, *st. comm.*) and much shorter in *D. vermicularis*. To the left of this part of the stomach adheres the caecum (*st. coec.*), with its spiral septa (*rad.*). Only the anterior part of the glandular stomach has spiral folds in *D. sagitta*; the posterior part is situated on it like a sac.

The muscular stomach (*st.*) is distinctly differentiated from the part of the stomach into which
295 the esophagus opens. It is long and in *D. vermicularis*, has a caecum (*st.'*) which is situated slightly to the left. The posterior end of the muscular stomach with its caecum was curved ventrally in my specimen. I do not know whether this is accidental or constant. I did not find a caecum in *D. sagitta*, unless the posterior process of the stomach be considered as such.

The mid-intestine (Figure 5, *int.*) exits the stomach at the level of the opening of the esophagus. It passes below the liver and then without distinct boundary into the rectum; longitudinal folds shine through the rectum. The anus forms a slit with two lips and anal appendages (Figures 3, *app. an.*), which are lanceolate in *D. vermicularis*; their two lamellae are of the same size and are supported by a median muscular stalk.

The ink sac (*atr.*) is short in *D. sagitta*, longer and pear-shaped in *D. vermicularis*. It opens dorsally into the rectum near the anus.

The liver (*hep.*) is spindle-shaped and forms an angle of about 45° with the longitudinal axis of the body (Figures 4, 5). Its capsule has a metallic sheen in the preserved specimen of *D. vermicularis*, while it was bright red in the live *D. exophthalmica*. The liver opens ventrally in its posterior third into two hepatic ducts, each with a broad, oval, pancreatic lobe (Figure 4, *pancr.*). The right lobe has the form of a hammer, the shaft being represented by the relatively wide efferent duct; the left lobe consists of two lobes which form an angle. The ducts surround the beginning of the mid-intestine and open together in the caecum. If one pancreatic lobe is folded aside, the short efferent duct of the liver becomes visible and near it the pancreatic vein, which opens directly into the sac of the vena cava. If both pancreatic lobes are folded in the anterior direction, the two converging hepato-pancreatic ducts are visible; the gastric vein passes over these ducts until it, too, opens in the sinus of the vena cava.

Vascular system. Examination from the ventral side shows the large vena cava (*v. c.*). That of *D. vermicularis* turns ventrally between the two olfactory tubercles and forms a small caecum at its exit from the cranium. It then passes to the surface and between the two adductors behind the funnel and anus to the tip of the liver, and then curves to the right around the liver. The vena cava opens into a sac covered with venous appendages and receives on the left side a smaller sac formed by the confluence of the two hepatic veins (*v. hep.*). The hepatic veins originate at the border of the anterior third of the liver, below the "anlage" of the luminous organs (Figures 3, 4, *v. hep.*); the left hepatic vein extends dorsal to the mid-intestine toward the right vein and unites with it on its entry into the sac. The vena cava

with its other sac then branches into two large venous sacs (*sacc. ven.*) which receive the large abdominal veins (*v. abd.*); these extend far posteriorly and receive small branches from the transverse muscular septa. There are also smaller sacs on the large sacs of the abdominal veins, which receive the pallial
296 veins (Figure 4, *v. pall.*) and then open in the spherical branchial hearts (*c. branch.*). The appendages of the branchial hearts (Figures 4, 5, *app. c.*) are situated laterodorsally and become only visible if the branchial hearts are folded upward. On the branchial hearts originate the branchial arteries (*a. br.*), which pass at first near the mantle veins and then divide into branches of the 1st and 2nd order on the gill. The branchial veins (Figure 4, *v. branch.*) widen into small, thin-walled sacs toward the heart (*c.*), which is bordered anteriorly and ventrally by the venous sacs and posteriorly by the anterior margin of the stomach. The aorta cephalica (Figure 4, *a. ceph.*) ascends dorsally behind the liver and reaches the surface at the level of the mantle ganglia. From the aorta cephalica branches the small arteria hepatica (*a. hep.*) to the liver. The arteria posterior (Figure 3, *a. post.*), which originates in an onion-shaped structure in front of the heart, passes on the ventral midline.

The very delicate **renal sacs** (*nephr.*) have oval outer openings (*ur.*).

Examination of the specimen of *D. vermicularis* from the ventral side showed whitish organs near the ink sac near the exit of the two hepatic veins. These organs are apparently the **ventral luminous organs** (Figure 3, *luc.*). They are situated exactly at the same place as the large luminous organs of *Chiroteuthis* earlier described herein.

The **genital conditions** of the specimens of *Doratopsis* examined show distinctly larval characters. Only after lengthy and painstaking examination did I locate the genital glands and the "anlage" of the gonoducts.

The genital glands (Figures 4, 5, *gen.*) of *D. sagitta* and *D. vermicularis* are small oval formations on the dorsal wall of the stomach. They are situated in *D. vermicularis* (Figure 4) at the point where the stomach curves anteriorly, and in *D. sagitta* almost at the posterior end of the stomach. In both specimens I found a small arterial vessel which extends from the "anlage" of the gonads dorsally toward the median plane and probably represents the arteria genitalis.

The gonoducts of *D. vermicularis* and *D. sagitta* (Figures 3, 5, *d. gen.*) are scarcely 0.5 mm long and situated directly behind the branchial heart near the entrance of the pallial vein into the venous sac. They are present only on the left side, which suggests that the specimens are males. Microscopical examination shows a thin undulate canal with indications of a later differentiation into a vas efferens, vesicula seminalis and spermatophore sac.

The only data available on the genital conditions were given by Weiss (p. 82). They are, however, so vague that all one can gather from them is that the specimen he examined was juvenile, probably
297 a male. In his illustrations Weiss designated a relatively large "anlage" as the genital gland. This is certainly an error, because he considered the sac-like terminal part of the stomach as the "anlage" of the genital gland.

The fact that the specimens of *Doratopsis* examined show despite their relatively large size larval characters in their genitalia supports, in my opinion, the view of Ficalbi that *Doratopsis* is the juvenile form of *Chiroteuthis*. As mentioned earlier, Pfeffer (1900, p. 185) countered this view with a number of arguments which were certainly justified. Let us therefore briefly examine Pfeffer's objections. He states:

1. "The largest *Doratopsis* known have greater mantle length than the fully grown *Chiroteuthis*."

This is correct for the oldest *Doratopsis* and the youngest *Chiroteuthis* illustrated by Ficalbi (Plate I, Figures 2, 4). In general, however it is untenable. As shown by the measurements given above, the male specimen of *Chiroteuthis* examined has a mantle length of 84 mm, while the largest *Doratopsis* described by Ficalbi, including the posterior margin of the fins, was 61 mm long.

2. "The eyeballs of the largest *Doratopsis* are less than half as wide as the eyes of a *Chiroteuthis* of the same mantle length."

Lengthening of the arms, and especially enlargement of the eyes takes place mainly during later stages of growth. The largest of my specimens of *Chiroteuthis* has an eye 24 mm wide, which is as large as the visceral sac, measured from the renal papillae. Analogues of such a delayed enlargement of the eyes are present not only in other organisms but also in other Cephalopoda.

3. "The two genera differ distinctly in the dentition of the sucker rings of the arms and tentacles."

This applies to the larvae of all Decapoda. The more characteristic the suckers of the adult animal, the greater the differences. Thus, the hooks develop from suckers of larvae which at first do not have a larger median tooth.

4. "The locking cartilages of the two genera differ sharply in every detail: form, fusion with the posterior margin of the funnel, the formation of tragus, antitragus and groove and the locking cartilage of the mantle. All these characters comprise constant, distinct differences between the two genera. Particularly characteristic, however, is the straight longitudinal ridge, which in *Doratopsis* extends constantly through the whole groove of the cartilage but is absent in *Chiroteuthis*. The opposing part of this ridge is distinctly
298 present on the locking cartilage of the mantle of *Doratopsis*, so that this cartilage, too, differs sharply from the corresponding part in *Chiroteuthis*."

This objection can be answered by stressing the great variability of the locking cartilage in all specimens of *Doratopsis* examined. Moreover, a straight longitudinal ridge in the groove of the cartilage is—at least in my specimen of *Doratopsis vermicularis*—not recognizable.

Pfeffer admits that the specimen described by Ficalbi, which shows intermediate characters between the two genera, can be interpreted morphologically only as a hybrid. Before we can accept so arbitrary an assumption, we have to consider the fact that the differences between *Chiroteuthis* and *Doratopsis*—however great their prominence in the extreme cases—are compensated by the intermediate stages.

What determined my view is the fact that all specimens of *Doratopsis* examined proved to be larvae in terms of the development of their genitalia. The genital glands and gonoducts are so small that only if one is very familiar with the anatomy of these animals can one find them at all. The genitalia are far more retarded in their development than the genital "anlagen" of juvenile animals which have repeatedly been described in this study. If the specimens are larvae, they can only belong to *Chiroteuthis*. The oldest specimens of *Doratopsis*, as described by Verrill and, later, Ficalbi, already have luminous organs on the ventral arms, and that, in the arrangement found only in *Chiroteuthis*. The large ventral luminous organs apparently develop even earlier, as the examination of *D. vermicularis* revealed. I admit that the differences between *Doratopsis* and *Chiroteuthis* are rather significant, must however stress that both as concerns the external habitus and the inner organization, they do not go beyond the changes which take place during postembryonic metamorphosis. For example, the differences between young larvae of *Pterygioteuthis* and the adults are, in my opinion, much greater than those between *Doratopsis* and *Chiroteuthis*. At least the habitus is the same in this case, while all characters typical for the mature *Pterygioteuthis* develop only during the postembryonic metamorphosis. If one furthermore considers

that younger specimens of *Chiroteuthis* will generally resemble *Doratopsis*—a fact also emphasized by Pfeffer—and that, as already stressed in connection with the description of *Ch. imperator*, the genitalia develop surprisingly late, then I would certainly not reject the view of Ficalbi as categorically as did Pfeffer and Hoyle.

Oegopsida consuta CHUN

Funnel apparatus (ventral wall of funnel, collaris and depressors) fused with mantle. Funnel valve absent.

Cranchiaeformes STEENSTRUP, 1861

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9. Family **Cranchiidae** PROSCH, 1847

Loligopsidae 1835–48, D'ORBIGNY, *Céph. acét.*, p. 320.
Cranchidae 1847, PROSCH, *Nye Cephalop.*, p. 71.
Cranchiadae 1849, GRAY, *Cat. Moll. Brit. Mus.*, p. 37.
Cranchiaeformes 1861, STEENSTRUP, *Overblik*, p. 70(2).
Taonidea (Desmoteuthidae) 1881, VERRILL, *N. Am. Ceph.*, pp. 300, 431.
Loligopsidae 1834, DE ROCHEBRUNE, *Mon. Loligopsidae*, pp. 1–21.
Cranchiaeformes 1886, HOYLE, *Rep. Chall. Ceph.*, p. 44.
Cranchiaeformes 1900, JOUBIN, *Rés. Camp. Monaco*, p. 15.
Cranchiidae 1900, PFEFFER, *Syn. Oeg.*, p. 188.
Cranchiidae 1906, CHUN, *Syst. Cranch.*, p. 82.

HISTORICAL REMARKS

D'ORBIGNY (*Ceph. Acét.*, p. 320) created the Family Loligopsidae for the forms which are at present placed in the family Cranchiidae. He gave the following definition of the Loligopsidae:

> "Corps allongé, pourvu de nageoires arrondies ou ovales dans leur ensemble; point de crête auriculaire; yeux latéraux antérieurs, sans sinus lacrymal; membrane buccale très courte; ouvertures aquifères brachiales et anales nulles; tube locomoteur sans aucune bride supérieure, ni valvule interne; coquille interne cornée, généralement allongée, sans loges aériennes."

D'ORBIGNY placed the genera *Loligopsis, Chiroteuthis* and *Histioteuthis* in this family; it is no wonder that his diagnosis has to be superficial enough to justify his inclusion of such heterogeneous forms. Thus, the only decisive character given, the lack of a funnel valve, applies only to *Loligopsis* but not to *Chiroteuthis* or *Histioteuthis*.

300 The attempts of later workers to maintain the family Loligopsidae with a more precise diagnosis proved unsuccessful, and so this name finally fell into disuse.

Prosch (1847) was the first to make an attempt to give the specific character of the Cranchiidae a systematic expression. Out of the odd collection comprising the family Teuthidae, which was established by Owen (1836), he separated a family named Cranchidae. It contains the genus *Cranchia* and the genus *Owenia* which Prosch was the first to describe. That he correctly recognized the major character of the new group is shown by his diagnosis of *Cranchia*: "Saccus cum tubo continuitate integumentorum conjunctus" (p. 71).

A more restricted definition of the Loligopsidae was given by Gray (1849), who reduced them to the genus *Loligopsis* and established the family Chiroteuthidae for *Histioteuthis* and *Chiroteuthis* (p. 42). Gray (pp. 36, 37) placed the Loligopsidae next to the Cranchiadae and united them in a common section with the following diagnosis:

Section I. Ventral side of mantle supported by two internal fleshy bands.

I. Cranchiadae. Eyes covered with the skin. Siphuncle with a valve.

II. Loligopsidae. Eyes naked. Siphuncle simple.

Each of these families consists of a single genus, *Cranchia* and *Loligopsis*, respectively.

This system of Gray represents an advance since it stresses the major character of the cranchiids, i.e. fusion of the mantle margins with the body. Gray is however wrong in ascribing a funnel valve to the Cranchiidae and in considering the presence of eyelids to be a difference between the two families.

A revision of this system soon appeared. In a masterly treatise, Steenstrup (1861) united the two families of Gray into a single family, the Cranchiaeformes.

The characteristic fusion of the mantle is again considered as the main character of the family (the Danish diagnosis is given below in Hoyle's translation):

> "In the first place, the whole family Cranchiaeformes is characterized thus: 'The mantle is firmly united with the head at three separate points—namely, directly in the dorsal median line, and indirectly by means of the funnel on either side of it, where there is usually a movable sliding cartilaginous articulation or hook in other Cephalopoda.'"

It should be mentioned in this connection that the characteristic fusion of the mantle was first observed by Eschscholtz, whose observations were published by Rathke (1832, p. 151) in his work on *Perothis*. Rathke (*loc. cit.*) gave a correct if not exhaustive description of the fusion between mantle, funnel and dorsal side of the body. d'Orbigny (*Céph. acét.*, p. 320), unacquainted with the description of Rathke, described the "appareil de résistance" of *Loligopsis* as follows:

301 "Appareil de résistance, consistant au trois large brides ou attaches fixes placées au bord même du corps, qui le lient intimement à la tête, l'une cervicale ou dorsale à l'extrémité de la saillie médiane de la coquille. Les deux autres latérales inférieures au lieu où est ordinairement l'appareil intérieur mobile."

The ingenuity with which Steenstrup united the cranchiids into a single family despite the partly inadequate descriptions is evident from the following list of the species included:

1. *Cranchia scabra* Leach (*Philonexis eylais* d'Orbigny);
2. *Cranchia reinhardtii* (Steenstr.);
3. *Cranchia megalops* (Prosch);
4. *Leachia cyclura* Lesueur;
5. *Leachia ellipsoptera* (Adams and Reeve);
6. *Taonius hyperboreus* (Steenstr.);
7. *Taonius pavo* (Les.).

This list shows that Steenstrup included only forms which later research proved indeed to belong to the cranchiids. His work attracted little attention at first, possibly due to its language—Danish.

This explains why the group Taonidae, established by Verrill (1881, p. 431), is altogether identical with the Cranchiaeformes of Steenstrup. Verrill placed part of the cranchiids in this group under the name Desmoteuthidae and includes in this family the two genera *Desmoteuthis* Verrill and *Taonius* Steenstrup.

de Rochebrune (1883) proposed a rather disputable system of the cranchiids. He retained the old name Loligopsidae for the family and included there not only the cranchiids known at the time but also the juvenile forms of Chiroteuthidae under the name of *Doratopsis*. Objections to this system are discussed by Hoyle in his work *On Loligopsis and Some Other Genera* (1884). Furthermore, Hoyle (1886, *Chall. Rep.*) closely follows the views of Steenstrup and places the following genera in the Cranchiaeformes:

Cranchia Leach, 1817;
Liocranchia Pfeffer, 1884;
Taonius Steenstr., 1861;
Pyrgopsis de Rochebrune, 1884;
Leachia Lesueur, 1821, Steenstr., 1861;
Loligopsis Lamck., 1812.

Later investigators, notably Joubin (1900, p. 15) and Pfeffer (1900), tended indeed to follow the classification of Steenstrup.

The rich material of known and new cranchiids collected by our expedition induced me to delineate the system of the cranchiids more sharply, on the basis of external and internal characters (1906, p. 82). This revision will be given in the detailed description below. I mention here only that I place the genus *Galiteuthis* Joubin in the cranchiids. Joubin considers this genus as a representative of a separate
302 family, Cranchionychiae, because of the presence of hooks on the club (p. 292). I endeavor to prove that *Galiteuthis* is only the adult stage of *Taonidium* and resembles the other cranchiids in every respect.*

Cranchiidae Prosch 1847

Oegopsida in which the mantle is fused at three points with the neck and funnel.

Stripes of concrescence extend from the dorsal and the two ventral points of fusion which diverge at a sharp angle and are sometimes strengthened by externally visible cartilaginous ridges. The median ventral stripes of concrescence are caused by the fusion of the ventral lateral margins of the funnel, the others by a fusion of the lateral margins of the musculus collaris with the mantle. In addition, the musculus depressor infundibuli is fused with the mantle; this muscle broadens from the abdominal wall into a thin muscular lamella which reaches the sides of the mantle and the ventral margin

* The following systematic review does not include two genera that are only inadequately characterized: *Henseniotenthis* Pfeffer and *Helicocranchia* Massy.

According to Pfeffer (*Syn. Oeg. Ceph.*, p. 193), *Henseniotenthis* "differs from *Owenia* in that the suckers on the tentacles are present only on the club." Since the specimen is characterized as "very small", it is probably a juvenile form of *Teuthowenia*.

Helicocranchia has recently been described in detail and illustrated by Massy (*Ceph. Dibr. Ireland*, 1909, p. 35, Plate III). However, the description does not suffice to determine its systematic position. The genus is apparently closely related to *Desmoteuthis*, and mainly differs from it only in the form of the fins, which are longer than wide in *Desmoteuthis* while those of *Helicocranchia* are as long as they are wide and have a narrower dorsal base. Since this character is the only distinct difference between the two genera, it is doubtful whether it justifies the establishment of a new genus. At any rate, further material is necessary before the validity of *Helicocranchia* can be established.

of the collaris. The posterior margin of the depressor infundibuli is curved around the gills, dividing the dorsal mantle cavity into two chambers through which the respiratory water flows in, washes the gills, and enters the single ventral chamber. The collaris, which is fused at the lateral margins, is transformed into a strong pocket valve which effectively prevents back flow of the repiratory water.

Body rarely gelatinous and intensively pigmented (*Taonius*), usually fleshy, with sparse chromatophores, often completely transparent.

Arm apparatus weakly developed, the 3rd arms the longest. Arms rarely with wide protective membranes (*Cranchia*). Tentacles long, the stalk having biserial suckers. Arms and club of tentacles having suckers. The suckers of the median row of the club are transformed into hooks only in *Galiteuthis*.

Buccal funnel with 7 pillars, their attachments to the 1st and 2nd arms extending dorsally, those to the 3rd and 4th arms ventrally.

303 **Eyes rarely small (*Euzygaena*), usually large, rarely sessile (*Cranchia*), usually protruding or stalked.**

Head of stalk-eyed forms lengthened into a pillar between the stalks of the eyes and the arms.

Funnel without valve; median funnel organ with 3 ridges or lanceolate processes.

Gladius very narrow; it widens toward the posterior end of the body and has a terminal cone which is either short and spoon-shaped or long and slender.

Hectocotylization has been demonstrated so far in the genera *Cranchia*, *Liocranchia* and *Euzygaena*. It affects the right ventral arm in *Cranchia* and *Euzygaena*, the left ventral arm in *Liocranchia*.

I. Mantle with ventral cartilaginous ridges with cartilaginous tubercles. Luminous organs numerous (4 to 13) on ventral margin of eye; rarely absent. Caecum sac-shaped, larger than the stomach.

A. Ventral surface of mantle with two diverging cartilaginous ridges on each side. Fins moderately large, slightly projecting beyond posterior end of body, with indented posterior margin. Gladius with short, spoon-shaped cone. First and 2nd arms with protective membranes which are connected at the base like a sail. Pancreas situated at the confluence of the hepatic ducts.

1. Body bare, with conical cartilaginous tubercles only on the ventral cartilaginous ridges (*L. valdiviae* n. sp.) or also in the dorsal median line (*L. reinhardti* Steenstr.). Eyes protruding, with 4 uniform luminous organs. Stalk of tentacles with few suckers. Left ventral arm hectocotylized, with paired suckers proximally, with uniserial suckers distally. *Liocranchia* Pfeffer

2. Body covered with stellate cartilaginous tubercles. Eyes sessile, with 11 ventral and 2 small dorsal luminous organs. Arms with broad protective membranes. Stalk of tentacles with numerous suckers. Right ventral arm hectocotylized, strong, with a large keel; suckers usually in 4 rows, densely arranged at the tip which is curved dorsally. Third arms of male with small, densely arranged suckers at the tip. *Cranchia* Leach

B. Ventral surface of mantle having a single ridge with tubercles on each side. Fins forming together a circular disk which ends level with end of body. Posterior end of gladius ending in a slender cone. Pancreas widely separated from the liver, situated directly on the caecum at the end of the ductus hepaticus.

1. Eyes protruding, with 5 (*L. cyclura* Les.) or 8 (*L. eschscholtzii* Rathke) luminous organs. Head pillar short, wide. Tentacles lost in the adult animal. *Leachia* Lesueur

304 2. Eyes small, with long stalks, without luminous organs; stalks plump, ovoid. Head pillar long. Suckers of median rows of club of tentacle larger than those in the marginal rows. Third arms large. Right ventral arm hectocotylized, longer and thicker than the left, with a large keel and densely arranged biserial suckers.
Zygocranchia HOYLE (*Euzygaena* CHUN)

II. Mantle without cartilaginous ridges. One or two crescent-shaped luminous organs on ventral surface of eye. Caecum small; stomach large, usually consisting of 2 or 3 parts, the large posterior part sac-shaped and thin-walled, the anterior part with strong longitudinal folds.

A. Base of fins situated close together; body with pointed posterior end.

a) Club of tentacles without hooks.

α) Eyes protruding.

1. Body arrow-shaped, gelatinous, vividly pigmented. Fins in the form of long membranes, tapering anteriorly and posteriorly; posterior end of body projecting beyond the fins. Tentacles absent in the adult animal.
Taonius STEENSTRUP

2. Body goblet-shaped, fleshy, transparent, weakly pigmented. Fins oval, usually longer than wide, projecting beyond posterior end of body. Tentacles present. Pancreatic appendages covering the long ductus hepaticus, decreasing in size to the caecum of the stomach.
Desmoteuthis VERRILL

β) Eyes stalked.

1. Body cylindrical. Fins small, slightly longer than wide, slightly projecting beyond posterior end of body. Stalks of eyes long, slender; eyes ovoid. Head pillar long, pyramidal. Arms very small. Club of tentacle with large keel. The common sinus into which open the stomach, caecum, esophagus and mid-intestine is large. Stomach simple, not divided into parts. Pancreatic appendages extending to caecum of stomach. Two large luminous organs on ink sac.
Corynomma n.gen.

2. Body spindle-shaped. Fins small, long. Posterior end of body projecting beyond the fins. Eyes oval, situated on thick, short stalks. Arms moderately large. Club of tentacle not widened, without keel. Each of the 3 points of fusion of the mantle margin possesses two cartilaginous tubercles which branch like antlers. Pancreas extending in the caecum.
Crystalloteuthis n.gen.

3. Body sac-shaped. Fins very small, wider than long, projecting slightly beyond posterior end of body. Eyes oval, situated on short, plump stalks. Head pillar short, wide. Arms very small. Tentacles large. Club widened and keeled in older specimens. Pancreas situated compactly on the liver, not reaching the caecum.
Teuthowenia CHUN (*Owenia* PROSCH)

4. Body cylindrical. Fins small, wider than long, widely separated, situated on the lateral margins of the spoon-shaped cone. Eyes in the form of pointed shoes, produced ven-
305 trally into a long point. Stalks of eyes wide, long. Head pillar slender. Arms small. Club of tentacles not widened, without keel.
Sandalops n.gen.

5. Body arrow-shaped. Fins long, narrow. Posterior end of body needle-shaped, projecting beyond the fins. Eyes conical, their main axis longer than the transverse axis. Stalks of eyes wide, moderately long. Head pillar long, slender. Arms small. Tentacles with slightly widened club and narrow keel.

Toxeuma n. gen.

b) Club of tentacles with hooks.
Body arrow-shaped. Fins long, narrow. Posterior end of body pointed, projecting beyond the fins. Eyes ovoid, with very short and wide stalks. Head pillar short, wide. Arms moderately developed. Club of tentacles slightly widened, without keel, with suckers in 4 rows in young specimens (*Taonidium* PFEFFER). In older specimens suckers of marginal rows in middle of club disappear and some sucker pairs of the median rows are transformed into hooks. Carpal part differentiated, with adhesive knobs. Stomach long, divided into 3 parts. Pancreas compact, situated on the liver.

Galiteuthis JOUBIN

B. Fins widely separated. Body with rounded posterior end. Eyes situated on large, plump stalks.
Body sac-shaped. Fins small, rounded, tapering toward the base. Posterior end of gladius transformed into a transverse rod which widens gradually laterally and supports the base of the fin with its shovel-shaped ends. Eyes large, oval, with a ventral pointed process above the large luminous organ. Stalks of eyes, long, broad, lyre-shaped. Head pillar long, slender. Arms small. Tentacles very large; stalks of tentacles with numerous biserial suckers their whole length. Club slightly widened, very long, keeled. Sac-shaped terminal part of stomach curved anteriorly and ventrally. Pancreas compact, horseshoe-shaped, situated on both sides of the liver, which protrudes far into the respiratory cavity.

Bathothauma n. gen.

External characters

No other family of Oegopsida is distinguished by so peculiar characteristics as the Cranchiidae. Since I am able to contribute the description of 5 new genera to the knowledge of the family and since the anatomical study of most of the important forms has led me to new conclusions, it seems in order to preface the description by a general characterization of their organization.

The most important character of the Cranchiidae, transformation of the funnel apparatus, has been described in detail in the "Comparative Review of the Organization" (pp. 6–9). The biological function of the concrescences of the ventral wall of the funnel, the collaris and the depressors with
306 the mantle is that of directing the flow of water for respiration and movement into more strictly defined channels within the mantle cavity than is the case in other Cephalopoda. The fusions form two dorsal streams of water, which flow from the anterior to the posterior part of the body, leave through the "spiracula" to wash the posteriorly situated gills and then unite into a ventral current in the reverse
307 direction and leave through the funnel. As reported by RATHKE (1832, pp. 151, 152), already ESCHSCHOLTZ observed nearly 90 years ago in *Leachia* (*Perothis*), the two dorsal "respiratory sacs" through which water simultaneously enters, passes to the gills and then is ejected through the funnel.

The Cranchiidae show a striking variety of forms. Some of them are plump, sac-shaped (*Bathothauma*, *Teuthowenia*), others slender and arrow-shaped, this finding its extreme expression in the genus *Toxeuma*. All conceivable gradations between these contrasting forms are found in the other genera.

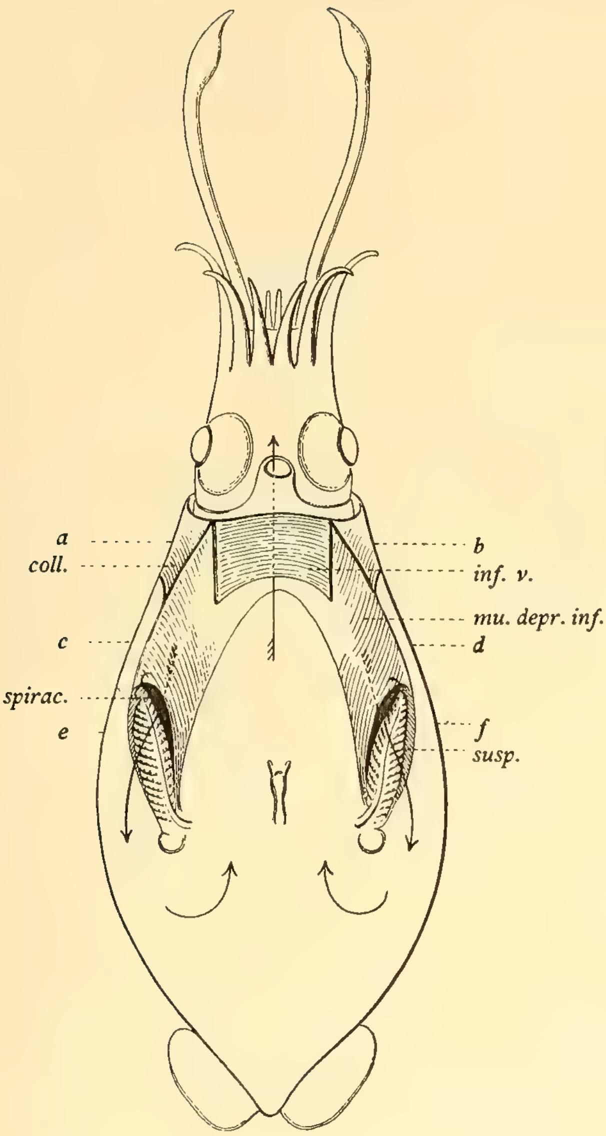


FIGURE 29. *Cranchia*, ventral side

a . . . b plane of section in Figure 4 (p. 8)
c . . . d plane of section in Figure 5 (p. 8)
e . . . f plane of section in Figure 6 (p. 8)

coll. musculus collaris; *inf. v.* ventral wall of funnel; *mu.depr. inf.* funnel depressors; *spirac.* spiraculum; *susp.* suspensory ligament of gill.
The arrows indicate the direction of the flow of water.

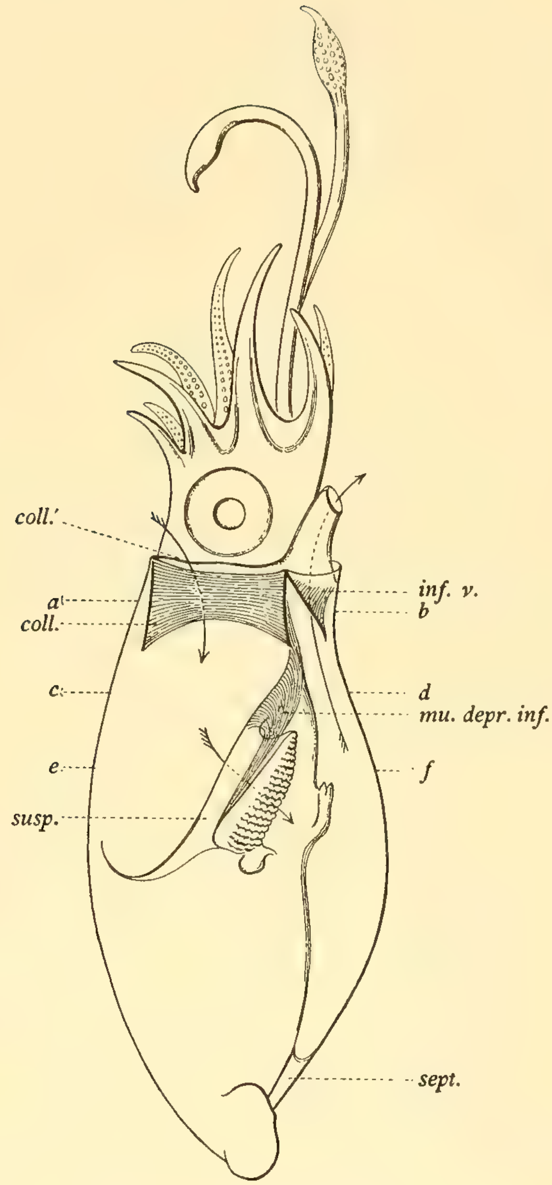


FIGURE 30. *Cranchia*, right side

a . . . b plane of section in Figure 4 (p. 8)
c . . . d plane of section in Figure 5 (p. 8)
e . . . f plane of section in Figure 6 (p. 8)

coll.' insertion of collaris on the head: *coll.* lateral lobe of collaris, which is fused with the mantle; *mu. depr. inf.* funnel depressor; *sept.* mantle septum; *susp.* suspensory ligament of gill.
The arrows indicate the direction of the flow of water.

The differences in characteristic form are produced mainly by the shape of the posterior end of the body, which is broad and rounded in *Bathothauma*, spindle- or arrow-shaped in *Galiteuthis*, *Taonius* and *Crystalloteuthis*, and needle-shaped in *Toxeuma*.

The form of the fins varies according to that of the posterior end of the body. The fins of *Bathothauma* are rounded and widely separated, connected by the broadened gladius. In the other genera, the dorsal bases of the fins are situated closely together, nearly contiguous at the posterior end of the body, and diverge in an acute angle which opens out anteriorly (*Cranchia*). Singly, the fins are in that case nearly semicircular and end level with the pointed end of the body or project slightly beyond it (*Liocranchia*, *Desmoteuthis*). In other cases, the fins are almost contiguous at their dorsal base and are nearly circular together (*Leachia*, *Euzygaena*).

If the dorsal bases of the fins are nearly parallel and much longer than the width of the single fin, each fin forms an oblong membrane. In the arrow-shaped forms (*Galiteuthis*, *Taonius*, *Toxeuma*), this membrane often occupies a large part of the mantle and ends anterior to the pointed end of the gladius.

Head

The head is either short and wide (*Cranchia*, *Desmoteuthis*) or very narrow and long, as in the forms with stalked eyes. Intermediate between these extremes are forms in which the eyes are situated on short stalks or protrude from the body. The anterior part of the head of stalk-eyed forms is markedly elongate between the base of the stalks and the arms apparatus. I name this part "head pillar". It contains two muscular cords, a dorsal and a ventral, so that it is sometimes almost quadrangular. The dorsal muscles originate on the anterior margin of the collaris and extend to the base of the 1st and 2nd arms; the ventral muscles originate on the dorsal posterior wall of the funnel and extend to the base of the 4th arms and the tentacles. In *Euzygaena* the dorsal muscles are narrower than the ventral ones; *Bathothauma* shows the opposite condition. The dorsal muscles of *Bathothauma* and *Sandalops* extend into a ring-shaped muscle which surrounds the stalks of the eyes at their bases, anterior to the col-
308 laris and is ventrally in front of the funnel closed. In the other species this muscular ring is not sharply differentiated from the collaris or from the funnel wall. I name the dorsal muscles which extend at the end of the musculus retractor capitis "musculus pilaris superior" and the ventral muscles, "M. pilaris inferior".

It is the form of the **eyes** that determines the physiognomy of the head of the Cranchiidae. Sessile eyes of relatively large size are characteristic for the genus *Cranchia*; *Taonius*, *Desmoteuthis*, *Liocranchia* and *Leachia* have protruding eyes, while stalked eyes are found in the most highly differentiated forms. The stalk may be short and thick (*Teuthowenia*, *Crystalloteuthis*, *Galiteuthis*), it may form an oblong oval (*Euzygaena*), or a short pillar (*Sandalops*); *Corynomma* has extraordinarily long, narrow stalks, and *Bathothauma* plump and nearly lyre-shaped ones.

The eyes are usually large; only in *Euzygaena* are they relatively small. The eyeball of the genera *Cranchia*, *Leachia* and *Liocranchia* is almost spherical. The other genera have an oval or ovoid eyeball, sometimes (*Bathothauma*) with a distinct, pointed ventral process (*Sandalops*) (Plate LVI, Figures 6, 8, 9). Only the eye of *Toxeuma* is almost telescopic because it is much longer than wide (Figure 10).

The ganglion opticum is disc-shaped in the genera with sessile or protruding eyes; it is spherical in the forms with stalked eyes and divided in two halves by a groove at the entrance of the nervus opticus. The two nervi ophthalmici are distinctly visible in the stalks near the optic nerve (Plate LVI, Figure 9).

The rounded opening of the lid may be withdrawn from the lens on strong contraction. Since the lid margin is surrounded by strong circular muscles, it may, in preservation, become closed completely and sometimes bloated like a hernia. An eye sinus is only weakly indicated.

The **olfactory tubercles** of the Cranchiidae have been mentioned by some observers, e.g. Pfeffer for *Teuthowenia*, *Leachia*, *Liocranchia* and *Cranchia*. They are described as rounded, sessile knobs;

in *Desmoteuthis*, however, they have a long, threadlike stalk. I found olfactory tubercles in all the genera mentioned. They are situated on the ventral outer margin of the eye and have very short stalks in a mature specimen of *Liocranchia* and in *Desmoteuthis pellucida* (Plate LIX, Figure 7). Only in *Taonidium* (Plate LIV, Figure 11), did I find olfactory tubercles with a long stalk, but in the other forms with stalked eyes—excepting *Euzygaena*, which has a sessile tubercle at the level of the anterior margin of the ganglion opticum—I was unable to detect long stalks with any certainty.

Arm apparatus

Many authors, e.g. Pfeffer, describe the arms of Cranchiidae as "embryonic." This may be due to the fact that most of the specimens observed were juveniles and give the impression that the arms
309 show primitive characters. Examination of adult animals shows that the arm apparatus is certainly not embryonic, although it may remain unusually small and has a relatively simple structure. The 3rd arms are usually larger than the others and particularly large in *Euzygaena*. The arms always bear 2 rows of suckers, never hooks. All protective membranes on the arms of our large and magnificent specimen of *Cranchia* are well developed and show the characteristic transverse muscular bridges. This is also the case in *Desmoteuthis* and, to a lesser degree, in several other genera of Cranchiidae. In the adult *Cranchia*, the protective membranes of the first two pairs of arms are connected at the base, so that they form a sail (Plate L, Figure 1). On the other arms this broad basal connection by protective membranes is absent. Between the 2nd and 3rd arms, however, there are broad outer membranes; another outer membrane extends from the 3rd arms, passes round the tentacles and ends in the basal part of the swimming membrane of the 4th arms.

Tentacles have not been found in the genera *Leachia* and *Taonius*. They are apparently regularly lost in these forms, just as in *Octopodoteuthis*. Joubin (1905, No. 33) reports that a number of females of *Leachia* were collected on a cruise of the *Prince of Monaco* between the Canaries and the Azores. They had deposited their eggs and were swimming about exhausted, on the surface. None of them had tentacles. However, as the stumps of the tentacles were distinctly visible, it has to be assumed that the tentacles are lost not during youth but later in life.

The tentacles of the other genera of Cranchiidae are always well developed and sometimes large. The development of the tentacles is in general the stronger the less the arms are developed, and vice versa. The two extreme conditions are represented respectively by *Bathothauma* with their huge tentacles and delicate arms and *Cranchia* with their relatively large arms and short tentacles.

The club of long tentacles, like those in the forms with stalked eyes, is little differentiated from the stalk. The clubs of *Cranchia* and *Desmoteuthis*, on the other hand, are markedly widened. The stalk is cylindrical at the base; its inner side is slightly flattened and widens gradually distally, where it passes into the disc of the club. A shallow median groove passes on the inner side of the stalk.

The **club** is usually dorsally curved, like a sickle; a keel is present only at the distal end (it is absent in *Galiteuthis*) and is more or less distinctly displaced toward the concave dorsal surface. Protective membranes, which are recognizable by their muscular bridges, are always present, although they may be very narrow and indistinct at the dorsal margin.

The suckers are arranged in 4 rows on the hand part of the club. The proximal half usually bears
310 larger suckers, but this difference in size may almost vanish in long clubs (*Bathothauma*). Characteristic for the genus *Euzygaena* is the small size of the suckers of the marginal rows, as compared to

those of the median row (Plate LII, Figure 2). This is also the case in young specimens of *Taonidium*, which are of special interest in this respect because some of their median row suckers are in the process of becoming transformed into hooks. The marginal suckers later disappear, so that the club bears only the characteristically strong hooks (Plate LIX, Figures 5, 6). The hooks are present only in the proximal and middle part of the club, the distal part retaining the rows of 4 suckers. Joubin, who described the adult specimens of *Taonidium* as *Galiteuthis*, even established the family "Cranchionychiae," because of the presence of hooks. However, the systematic value of this isolated occurrence of hooks has been overestimated in my opinion, because the whole organization of the Cranchionychiae fits definitely in with that of the other Cranchiidae.

The stalk of the tentacle of all Cranchiidae always bears small suckers. They are definitely present also in the young and adult *Liocranchia*, in which Pfeffer failed to find them. The suckers are stalked and arranged always in 2 rows, either alternating in a zigzag pattern or in pairs at the same level. In the former case, the rows may be so stretched that one gains the impression of a uniserial arrangement (Plate LI, Figure 12, *Liocranchia*). On careful observation, one can discern a zigzag alternating pattern also if the suckers are arranged in pairs at about the same level (Plate LV, Figure 9, *Corynomma*). This is because the successive groups of two suckers are displaced, regularly alternating, to right and left. Examination of well-preserved tentacles shows that this apparently biserial arrangement of the suckers developed from an arrangement in 4 rows. This can be proved not only embryologically (Plate LV, Figure 7, tentacle of a young *Corynomma*) but also by a study of the area where the stalk and club are connected. At the point where the hand part of the club passes into the distal part of the stalk, it is evident that the oblique rows of 4 suckers become the steeper and the more extended the further they advance toward the stalk. Since the adjacent suckers of two successive rows of 4 suckers are situated at about the same level, an alternation of the successive pairs results. This is shown diagrammatically in Text Figure 31, in which the oblique rows of 4 suckers are indicated by dotted lines.

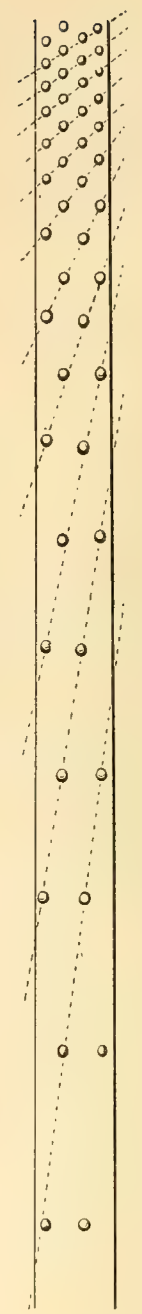


FIGURE 31. Diagram showing the development of biserial groups of suckers from elongated quadriserial groups of suckers.

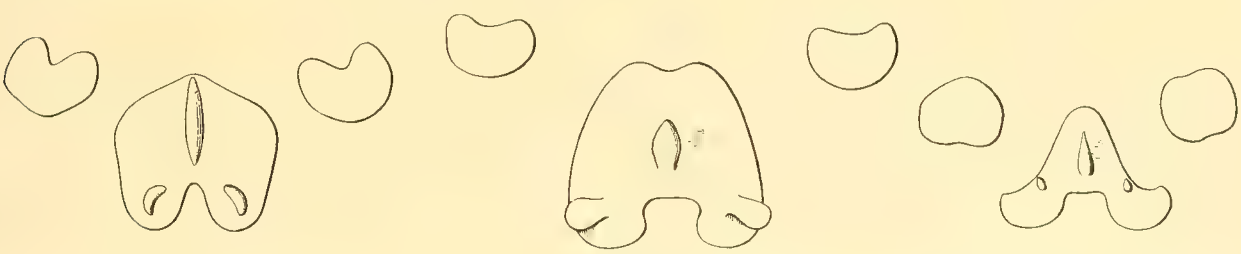
311 Furthermore, in *Galiteuthis* a carpal part is developed, proximal to the hooks (Plate LIX, Figure 5). Younger specimens (*Taonidium*) show distinctly that this carpal part, too, has developed from groups of 4 suckers between which delicate adhesive knobs can be detected (Figure 6). In most Cranchiidae these knobs can be seen also on the stalk to alternate regularly with the small suckers; but this is discernible only under good illumination. These adhesive knobs of the stalk apparently developed by the suction of the suckers of the opposite tentacle.

The **buccal funnel** is usually of moderately large size, with 7 buccal pillars. The dorsal pillar is single, the two ventral pillars are situated close together. From the dorsal pillar extend two attachments to the dorsal margin of the base of the 1st arms; an attachment to the ventral margins of the 4th arms extends from each of the ventral pillars. The other attachments pass dorsally on the 2nd arms, ventrally on the 3rd arms. The muscles of attachment of the tentacles are short and deeply situated. The buccal cone is usually raised in the form of a chimney; the thick inner lip is fluted, but the narrow outer lip is smooth.

Funnel

The **funnel** is always large; it is either long (*Leachia*) or hangs down with a flabby opening. The funnel adductors are barely visible from the outside; particularly characteristic is the absence of a funnel valve. This was stressed already by d'Orbigny (Ceph. Acét., p. 320) for *Loligopsis* and his data were later confirmed by Brock (1880, p. 37) and Hoyle (1886, p. 187). Since I found no funnel valve in any of the genera examined, not even in *Desmoteuthis*, for which Pfeffer (p. 191) described it, its absence is apparently an important character of the Cranchiidae.

The **funnel organ**, which is always well developed, was described by Verrill (1881, Plate 54, Figure 2 d) for *Desmoteuthis tenera*. It consists of two lateral lobes on the ventral side of the funnel, which are usually oval. There is also a dorsal median lobe, behind which the vena cava passes to the ventral surface. The median lobe may be shovel- or helmet-shaped or have the form of spectacles (*Batho-*
312 *thauma*). Its median part usually bears a lanceolate or tongue-shaped process and a lateral process on each side. Some characteristic funnel organs are illustrated in Figure 32. The processes of the median lobe of *Corynomma* (a) show a primitive condition because they have ridges, of which the median is long and the lateral are sickle-shaped. The median process of *Crystalloteuthis* (c) forms a lanceolate tongue, while the lateral processes are small and conical. In *Desmoteuthis* (b) and *Galiteuthis*, all 3 processes project in the form of spatulate tongues.



a b c

FIGURE 32. Funnel organs of Cranchiidae:

a *Corynomma speculator*; b *Desmoteuthis pellucida*; c *Crystalloteuthis glacialis*.

Luminous organs

Already early observers of Cranchiidae mentioned strongly refractile structures on the ventral margin of the eye. We know today that these are luminous organs. Rathke (1832, p. 169) described them for *Leachia* (*Perothis*), and Grant (1833), too, observed them in *Leachia*. Pfeffer (1900, p. 190) mentioned the luminous organs of *Cranchia* and *Liocranchia*. More recently, Joubin (1905) gave a detailed description of the luminous organs of *Leachia*, including their fine structure. Since I am able to extend out knowledge on some of the main aspects of occurrence of these organs, a fuller description of their structure will be given in context with the description of the particular genera; at this point I confine myself to a few data on their distribution.

The simplest condition is present in *Liocranchia*, which has 4 organs of uniform structure on the ventral margin of the eye (Plate LX, Figure 7). In preserved specimens they appear as whitish bodies surrounded by a shiny golden rim which widens slightly toward the anterior margin of the eye. *Leachia cyclura* has 6 organs. According to Joubin, 5 organs are situated on the ventral margin, the 6th close

to the lens. Eight organs are present in *Leachia eschscholtzii*, according to RATHKE. In a specimen of *Leachia* from the environs of Borneo I also found 8 organs, so that this specimen is apparently another *L. eschscholtzii*; six organs are situated on the ventral outer margin, the other two more inward, near the lens.

Cranchia has as many as 13 organs on the eyes (Plate L, Figures 4, 5). Seven form an outer circle which passes in a curve into an inner circle of 4 organs. There are also two small organs near the dorsal margin of the lid. The large organs of the outer row are adjoined by conical mirrors with a weak golden sheen.

The luminous organs of the eyes of the above-mentioned genera of Cranchiidae were observed already in earlier studies, but apparently no one noticed the huge luminous organs on the ventral surface of the eyes which are probably present in most of the other genera of Cranchiidae. They are
313 sickle-shaped or crescentic and are present either singly or in pairs, covering a large part of the ventral surface of the eyes. If two organs are present, the anterior is situated in a concavity of the posterior organ. I found these organs first in *Desmoteuthis* (Plate LIV, Figures 7, 8) and later also in *Galiteuthis* (Plate LIX, Figure 11), *Bathothauma, Teuthowenia* (Plate LVI, Figures 5, 9) and *Crystalloteuthis* (Plate LIII, Figure 7). The specimens of the other genera at my disposal were young animals, in which the organs are indistinct, but I am fairly certain that such organs are present also in the genera *Toxeuma* and *Corynomma*. In any case, it is noteworthy that if these large organs are present, the small organs mentioned above are always absent.

Finally, I should like to mention an interesting condition found only in *Corynomma*. During examination of the viscera, I observed a peculiar pattern of ear-shaped swellings at the apex of the liver which is situated on the ink sac (Plate LX, Figure 13). This proved to be the free outer surface of unusual organs resembling those described in the Chiroteuthidae. As these organs have reflectors, I consider them as luminous organs (Plate LX, Figures 14–16). I do not know whether such organs, which are deeply embedded in the liver parenchyma near the rectum, are present also in other genera of Cranchiidae; sections of the anterior part of the liver of a larger specimen of *Cranchia scabra*, at least, showed no such organs.

Consistency and coloration of the body

The strongly muscular mantle and the arms of almost all Cranchiidae have a fleshy consistency. Only the mantle of *Taonius pavo*—which, admittedly, I know only from a specimen found in the stomach of a grey albatross—has a gelatinous consistency. A gelatinous consistency is especially characteristic for the head of the Cranchiidae with stalked eyes, including the genus *Leachia*.

A vivid coloration is rare in the Cranchiidae. It is characteristic for *Taonius pavo* and gave it its species name. If chromatophores are present on the mantle, they are usually symmetrically arranged and widely separated (*Desmoteuthis*, *Euzygaena*). Even if they are more densely arranged, as in a large specimen of *Cranchia*, they affect the nearly complete transparency of the mantle only very little. The forms with stalked eyes are particularly transparent. This is well illustrated in a specimen of *Desmoteuthis* from the southern Atlantic. The mantle was covered by a thin layer of mucus, that can still be detected in a preserved specimen, even when parts of its mantle are placed in pure water, due to its becoming bloated.

314 ## Inner anatomy

There is so little information on the anatomy of the Cranchiidae that I undertook an examination of the inner organization of those precious specimens—as far as was possible without destroying their value as types.

Only a few authors have dissected the valuable material. The earliest and still most reliable anatomical study of the Cranchiidae was published by H. RATHKE on *Perothis* (*Leachia*). RATHKE's work appeared in 1833; it was so far ahead of its time that later investigators either failed to understand it or paid it only superficial attention. It is unfortunate that BROCK (1880, p. 87) declared: "This work of an otherwise excellent observer is full of inaccuracies, ambiguities and errors." If BROCK had examined the anatomy of the material of *Leachia* (*Perothis*) in his possession, he would have been convinced of the accuracy of most of RATHKE's data. The work of RATHKE contains a few errors, but precisely those structural details that were the very object of BROCK's severe criticism are correct. At any rate, RATHKE's work is far superior to the rather aphoristic communications of OWEN (1836) on *Cranchia*, of GRANT (1833) on *Loligopsis* (*Leachia*), of PROSCH (1847) on *Owenia* and of VERRILL (1881) on *Taonius pavo*.

Mantle complex

Opening of the mantle cavity by a ventral median cut shows its unusually large size in the Cranchiidae. In some cases, especially in juvenile specimens, the visceral sac is very small in comparison with the respiratory cavity. It is relatively large in the large specimen of *Cranchia*. In other forms, especially in the large *Bathothauma*, the posterior part of the visceral sac is very small (Plate LVIII, Figure 1) and tapers toward the posterior end of the body, sometimes like a thread. The abdominal wall is always thin and fused with the mantle along the dorsal median surface.

Except for the characteristic transformations of the anterior part of the mantle cavity described here earlier (pp. 6–9), the **liver** is particularly interesting. It is situated almost perpendicular to the longitudinal axis of the body and projects more or less far into the mantle cavity. The anus with its large appendages is situated at the ventral end of the liver. This is most striking in *Bathothauma*, in which the large, spindle-shaped liver projects far into the mantle cavity and has a thick muscular suspensorium at its anterior margin (Plate LVII, Figure 1, *lig.*) which forms a continuation of the abdominal wall. Only a few slender species, e.g. *Leachia* (Plate LII, Figure 5), have a more steeply situated liver which forms an acute angle with the longitudinal axis of the body.

A further characteristic of the Cranchiidae is the apparent absence of a median septum. Only careful
315 examination of an entirely intact specimen reveals it, in the posterior part of the body, anterior to the end of the tail. I thus found the septum in the large *Cranchia* (Plate XLIX, Figure 7) and in *Taonidium*. On the anterior margin of the septum extends the arteria pallialis, which branches from the arteria posterior and is therefore displaced far posteriorly.

The two renal openings are visible on both sides of the liver; they project like a chimney in some genera. The branchial hearts, and in many cases the large, very long branchial arteries and branchial veins, are distinct, and so is the vena cava, which often has an undulate course—probably as a result of preservation—and passes to the ventral surface directly behind the middle part of the funnel organ.

Intestinal tract

The intestinal tract shows some interesting conditions which are important for the determination of the relationship between the genera of the Cranchiidae. The intestinal tract of *Cranchia scabra* (Plate L) will be described as an example and compared with that of the other genera of Cranchiidae.

The esophagus (*oes.*) passes through the brain and then obliquely ventrally toward the posterior part. It extends to the left of the median septum (Plate L, Figure 7) that bisects the body cavity in the anterior part of the mantle. At the level of the dorsal apex of the liver it separates from the vena cephalica which surrounds it, forms there a whitish loop (*amp. v.*) and then opens into a slightly dilated sinus, a little to the right, far from the liver.

I made cross sections of the esophagus of a female *Cranchia* of medium size and can add the following details. Between its exit from the cranial capsula and its adherence to the ampulla of the vena cephalica, the esophagus contains longitudinal swellings, 7 in my specimen. They are covered with cuboid epithelial cells and are supported by cords of connective tissue which had slightly parted from the epithelium. The cords extend from an envelope of connective tissue which also attaches the esophagus to the median septum. This envelope has numerous internal longitudinal muscle fibers and external circular muscles. On them are situated the two sympathetic nerves and smaller vessels. The longitudinal swellings disappear in the area of the ampulla which surrounds the esophagus. The lumen of the esophagus widens before entering the gastric sinus. This is formed by the confluence of 4 parts of the intestine: the openings of the esophagus and caecum on one hand, and the beginning of the mid-intestine and stomach on the other. It is only weakly differentiated in *Cranchia*.

316 The stomach (Figures 6, 10, 11, *st.*) extends in line with the esophagus; it is small, muscular, with large longitudinal folds and is slightly constricted at the posterior end. The gastrogenital ligament (*lig. g. g.*) is visible to the posterior end of the gladius; it attaches and supports the genital gland, which is also in contact with the stomach in its anterior half.

The caecum or spiral stomach (*st. coec.*) opens broadly at the level of the entrance of the esophagus on its left side. The caecum is much larger than the stomach and has thin, delicate walls; it is divided, at least in the younger specimens of *Cranchia*, into an anterior part with spiral folds and a sac-shaped posterior part. The spiral folds are weakly developed, their spiral coils are scarcely indicated and they cover only a small part of the dorsal surface of the caecum (Figures 12, 13). The spiral folds converge toward a groove (*sulc.*) which is bordered by two swellings and passes to the mid-intestine. This groove is long in the large specimen (Figure 13). It is situated on the surface of the mid-intestine, which borders on the ductus hepato-pancreaticus. The wide opening of the caecum into the common sinus is bordered by two folds. One of these folds (*vel.*) has the form of a sail and extends straight posteriorly from the opening of the ductus hepato-pancreaticus on the wall of the caecum adjacent to the stomach. A second fold curves from the esophagus toward the posterior margin of the opening. This fold is small and was present only in the large specimen. The broad mid-intestine (*int.*) contains loose longitudinal folds. It crosses the esophagus, passing dorsally and slightly to the left of it toward the left half of the liver, where it is covered by the heart and the large vessels. It then turns toward the middle near the ventral apex of the liver and passes into the slightly narrower, short rectum (*rect.*) which surrounds the apex of the liver and opens in the anus between two transverse lips. The anal appendages are moderately large, lanceolate, slightly keeled, and the lateral lobes are nearly symmetrical.

Salivary glands. I prepared only the posterior gland. It forms a single spoon-shaped complex situated on the static organs.

The **liver** is spindle-shaped, slightly laterally compressed. It has a thick envelope which causes its

metallic sheen; but its colors in the live animal were less striking than they were in some other Cranchiidae. The posterior side of the liver bears two openings at the dorsal quarter, from which extend the short, wide hepatic ducts (Figure 8, *d. hep.*), which unite into the ductus hepaticopancreaticus (*d. hep. pancr.*) close behind the liver. At the point where the two ducts unite are situated the compact **pancreas glands** (*pancr.*) which consist of numerous lobes of different size. In *Cranchia* the left pancreatic gland is much larger than the right one (Figure 14). The pancreas covers the union of the hepatic ducts into the ductus hepaticopancreaticus, which forms a loop and then turns to the left and opens in the hood
317 of the spiral stomach. The confluence of the spiral folds forms a groove in which the hepatic and pancreatic secretions flow into the caecum, where the secretions are evenly distributed by the spiral folds.

The main characters of the intestinal tract of *Cranchia* are thus as follows:

1. The stomach and caecum are situated far behind the liver, so that esophagus, mid-intestine and hepatopancreatic duct are very long and adhere to each other, seeming to form a single duct; only a cross section reveals that it consists of 3 canals.
2. The caecum has thinner walls and is markedly larger than the stomach. Its spiral folds are weakly developed and cover a small area near the opening of the hepato-pancreatic duct.

A third but less important character is the fact that the pancreas forms two compact glands around the confluence of the hepatic ducts.

Comparison of the intestinal tract of *Cranchia scabra* with those of the other genera of Cranchiidae shows that *Liocranchia*, *Leachia* and *Euzygaena* resemble *Cranchia* in that the stomach and caecum are situated far from the liver, which causes the lengthening of the esophagus, the mid-intestine and the ductus hepato-pancreaticus. The caecum of these genera is also larger than the stomach and forms a thin-walled sac with weakly developed spiral folds.

However, the different genera have special characters of which only the most important will be mentioned here.

In *Liocranchia* the liver is situated much further from the stomach and caecum than in other genera of Cranchiidae. The 3 ducts which pass into stomach and caecum—esophagus, mid-intestine and hepatopancreatic duct—form numerous narrow spiral coils (Plate LI, Figure 13).

In *Leachia* and *Euzygaena*, on the other hand, these ducts are short and do not form spiral coils (Plate LII, Figure 5). Particularly marked in these two genera is the difference in size between stomach and caecum. The caecum forms a long, thin-walled sac, with a few spiral folds at the anterior end (Figure 7, *rad.*). The stomach may project beyond the posterior end of the caecum; it is divided into 2 parts, a long, tubular anterior part and a very short, sac-shaped, thick-walled end part which contains strong longitudinal folds. The common sinus of the 4 parts of the intestine protrudes in *Leachia* much more distinctly than in any of the other Cranchiidae, because the trumpet-shaped entrance to the stomach is sharply delimited by a transverse sail-shaped fold (Figure 6).

The pancreas of the above two genera shows an important character. As already described by Rathke, the pancreas (Figure 5, *pancr.*) is distinctly separated from the liver and opens directly into
318 the hood of the caecum, together with the ductus hepaticus (Figure 6). The pancreatic glands consist of slightly branched follicles which are larger in *Leachia* than in *Euzygaena*. They form two crescentic glandular complexes, which are almost contiguous dorsally, and open into the hood of the caecum by several large openings. All these characters suggest that *Leachia* and *Euzygaena* are related, despite several other differences.

As regards all other genera, they form a group that differs sharply from the genera described above, at least in one respect: the caecum of all the other genera is much smaller than the stomach. It does

not form a thin-walled sac, but is a thick-walled part of the intestine, usually consisting of an anterior "hood" and a posterior part of about the same size. The spiral folds are numerous and form dense lamellae which extend to the posterior part in a more or less distinct spiral.

The longitudinal fold which in *Cranchia* forms a sail-like process is here broad and swollen; but the fold extending from the opening of the esophagus to that of the caecum resembles that of *Cranchia.* The stronger development of the lamelliform spiral folds is probably connected with the large size of the groove of the mid-intestine which is bordered by thick, swollen margins. In *Bathothauma* this groove can be followed in the mid-intestine to near the liver.

The stomach forms a thin-walled sac in its greater part (*Corynomma*) which is divided more or less distinctly into 2 or, as in *Bathothauma*, 3 parts (Plate LVII, Figure 1). If it is divided into 3 parts, it resembles that of *Leachia* and *Euzygaena* in so far as it begins with a narrow anterior canal (*st.'*) which passes into a spindle- or onion-shaped part with very strongly developed longitudinal folds (st.″). This second part opens into the thin-walled, sac-shaped end part, which extends far posteriorly in the slender forms. These conditions have their most extreme form in *Bathothauma.* Here the first part of the stomach is very long and contains a few weakly developed longitudinal folds. The spindle-shaped second part is sharply distinguished by the strongly developed system of longitudinal folds. It passes with a trumpet-shaped opening (*x.*) into the thin-walled end sac which, in contrast to all other genera of Cranchiidae, is curved ventrally (Plate LVII, Figure 1, *st.*^{3}). Its slightly thickened apex is therefore situated near the caecum. A short distance before the caecum begins the filament of connective tissue which connects the end of the intestine with the posterior end of the body. This is a secondary displacement of the terminal part, which is also proved by the condition of the genital gland (*ov.*), which is curved horseshoe-like between the 2nd and 3rd parts rather than extending in a straight line, as in the other Cranchiidae.

319 The intestinal parts situated near the liver show the simplest condition in *Corynomma*, where it in many respects resembles that found in the Chiroteuthidae (especially *Doratopsis*). The esophagus opens in a large sinus which borders on the dorsal posterior surface of the liver and from which the mid-intestine extends anteriorly; the caecum is situated adjacent to this sinus, far from the opening of the esophagus.

The sinus of all other genera is narrower, because caecum and stomach are situated far posterior to the liver.

As a result, the esophagus, the beginning of the mid-intestine and the hepato-pancreatic duct extend for a varying distance near each other behind the liver. The genera *Teuthowenia*, *Galiteuthis*, *Bathothauma* and *Desmoteuthis* represent different stages of this condition. The extreme is found in *Desmoteuthis* (Plate LIV, Figure 12), in which these 3 parts form long ducts situated close together. The mid-intestine always forms a wide canal above which is situated, to the right, the narrow esophagus, and ventrally, the hepato-pancreatic duct (Plate LIV, Figure 13). The opening of the esophagus is always situated at the level of the opening of the small caecum.

The mid-intestine (*int.*) contains loosely arranged longitudinal swellings. It is situated broadly on the left posterior side of the liver and then passes into the rectum, which curves around the ventral apex of the liver and contains also longitudinal swellings. The boundary between mid-intestine and rectum of this genus is more distinctly marked than in *Cranchia.* The anal appendages are usually moderately large, rarely small (*Liocranchia*) and lanceolate. Their keel is more or less distinctly delimited from the lateral lobes; these are usually narrow, rarely wide (*Desmoteuthis*); they may be slightly asymmetrical, i.e. the inner lobe, which is sometimes directed dorsally, may be wider than the outer lobe (*Desmoteuthis, Corynomma*).

The liver (*hep.*) is spindle-shaped or ovoid. The extreme forms are found in *Teuthowenia* (Plate

LVII, Figures 6, 7), in which the liver is relatively short, ovoid, slightly laterally compressed, and in *Bathothauma* (Figure 1), in which the long, spindle-shaped liver projects far into the mantle cavity. In the live *Desmoteuthis*, the liver envelope had a metallic sheen (Plate LIII, Figure 1). The hepatic ducts extend posteriorly from the dorsal quarter of the liver (*Desmoteuthis*, Plate LIV, Figure 15, *o. pancr.*), curve around the mid-intestine, opening on its posterior side into the common hepato-pancreatic duct which is distinctly visible to the point where it opens into the caecum.

The pancreatic appendages show characteristic differences. They are situated in all the above genera directly at the exit of the hepatic ducts; in *Desmoteuthis* they form glandular follicles which decrease in size along the lateral stems and the common main stem of the long hepato-pancreatic duct (Plate LIV, Figure 12). This very characteristic condition is apparently present also in *Taonius pavo*. The drawing of the visceral sac of this species by VERRILL (1881, Plate XXXIX, Figure 1, *l.*) which shows a long tubular intestine, described as being covered on each side by rows of glandular follicles, is obviously the long ductus hepato-pancreaticus.

320 A similar, but less marked condition, is present in *Crystalloteuthis* (Plate LIV, Figure 18) and *Corynomma*. The anterior parts of the pancreatic glands are much larger than the following parts, which always extend to the caecum. All other genera, especially *Teuthowenia* (Plate LXII, Figure 6, *pancr.*), *Galiteuthis* and *Bathothauma*, have distinct, compact pancreatic glands which are present only on the beginning of the hepatic ducts. The pancreatic glands of *Teuthowenia* are curved on both sides around the posterior dorsal surface of the liver; those of *Bathothauma* are large, horseshoe-shaped and situated in the same position.

Nervous system

I did not make preparations of the brain and the nerves originating from it, in order to save the valuable specimens. However, I dissected the dorsal surface of the brain of a smaller specimen of *Cranchia* (Plate L, Figure 9) and found similar conditions as in the other Oegopsida. The specimen of *Cranchia* examined has a broadly heart-shaped ganglion cerebrale. This ganglion is nearly rectangular in a cleared specimen of *Corynomma* whose brain could be seen shining through; *Cranchia* has a very short head and its supraesophageal ganglion (*g. bucc. sup.*), therefore, almost approaches the brain. In forms having a long head pillar, this ganglion is situated further anteriorly.

The optic nerve is short in *Cranchia* and other forms with sessile eyes, and very long in forms with stalked eyes, according to the length of the stalk (*Corynomma*, Text Figure 11, p. 21; *Bathothauma*, Plate LVI, Figure 9). The ganglion opticum is bowl-shaped in *Cranchia*; it is nearly spherical in the forms with stalked eyes and shows a more or less distinct groove at the entrance of the nervus opticus (*Corynomma*, Plate LV, Figure 3; *Bathothauma*, Plate LVI, Figure 9). Another nerve which originates on the ganglion cerebrale is the nervus ophthalmicus superior, which is distinctly visible in *Cranchia* (Plate L, Figure 9). This nerve and the nervus ophthalmicus inferior have a characteristic course in the forms with stalked eyes (Text Figure 11). The gelatinous wall of the stalk contains dorsally and ventrally two nerves, one of which originates on the posterior lateral part of the brain, at the level of the nervus opticus, and the other on the anterior ventral surface (Plate LV, Figure 3). These two nerves correspond to the cords which CHÉRON named "nervus ophthalmicus superior" and "inferior." Both nerves resemble the optic nerve in that they are covered laterally their whole length with a stripe of ganglion cells and are accompanied by an artery and a vein. They form branches at the level of the eyeball.

Examination from the dorsal side also shows the lateral swellings of the ganglion viscerale; from these arise the nervi palliales which extend to the ganglia stellata. The latter are covered on all sides

with a thick envelope of ganglion cells, especially on the dorsal side, where they border on the gladius. The posterior halves of the ganglia stellata are connected by a broad transverse commissure. From
321 the ganglia stellata extend delicate nerves which branch in the mantle; the two large nerves of the fins, too, extend from the ganglia stellata; these nerves are in the slender forms particularly prominent on both sides of the gladius; they enter the anterior margin of the base of the fins. In *Bathothauma*, in which the fins are widely separated, the broadly diverging nerves are visible through the dorsal integument.

The ganglion gastricum is always situated to the right of the caecum and it, too, is completely enveloped by a thick cover of ganglion cells.

Vascular system

Arterial system

The heart of Cranchiidae is situated slightly on the right at the level of the posterior half of the liver, often somewhat oblique to the longitudinal axis of the body. It is cylindrical or spindle-shaped in *Leachia* and *Liocranchia*. In other forms, e.g. *Desmoteuthis* (Plate LIV, Figures 12, 14), it is inflated toward the atria and of irregular rhomboidal form. The axis indicated by the exit of the aorta anterior and posterior is usually longer than the transverse axis, but this is less marked in hearts of irregular form. To a lesser extent this applies to *Cranchia* and to a greater extent, to *Bathothauma* in which the heart is almost as long as it is wide.

Only two large vessels originate from the heart. The aorta cephalica originates at the dorsal end, the arteria posterior (abdominalis) on the ventral end. The arteria posterior is rarely slightly spindle-shaped at the base; the arteria anterior branches from it immediately after leaving the heart and then passes to the thin abdominal wall, continues posteriorly in the median line, branches into the short arteria pallialis at the level of the fins and then into the two arteries of the fins. The aorta cephalica is more or less spindle-shaped at the base; it curves around the dorsal apex of the liver on the right side, then extends anteriorly near the esophagus and branches behind the ganglion cerebrale (Plate L, Figure 9). I did not trace it further.

The arteria gastrica originates near the base of the aorta cephalica. It is distinct in *Leachia* (Plate LII, Figure 5, *a.g.g.*) on the hepatic duct, continues covered by the pancreas to the right near the ganglion gastricum and then branches along the caecum toward the stomach and the genital gland.

The arteria hepatica is always a single vessel which enters the liver dorsal to the right hepatic duct (Plate L, Figure 7; Plate LIV, Figure 12, *a.hep.*).

Near the arteria hepatica extends a vessel which previous observers failed to describe. I name it the "arteria dorsalis" (*a.dors.*); it may pass at the level of the arteria hepatica (*Leachia*), or else anterior
322 to it (*Cranchia*), or posterior to it (*Desmoteuthis*), on the posterior margin of the septum of the body cavity, extending toward the dorsal side of the mantle, where it furcates into branches which accompany the nerves of the fins and send off smaller vessels to the mantle.

Venous system

The vena cava becomes visible on the ventral surface of the body, directly behind the median funnel organ, and then extends straight to the apex of the liver. It often takes a markedly undulating

course, but this is probably due entirely to contraction during preservation. The vena cava describes always a wide circle, to the right side, around the anterior ventral half of the liver, thus reaching the area of the renal sacs to whose dorsal wall the vena cava adheres together with its adjacent veins.

The venous sacs in the area of the renal sacs are particularly distinct in the Cranchiidae. The vena cava forms a moderately large sac into which the sizable sacs of the vena hepatica open anteriorly and posteriorly (Plate L, Figures 6, 7, 14; Plate LIV, Figures 12, 14, 15, 18). They are always situated to the right of the mid-intestine (*sacc. v. hep. ant.* and *post.*). The vena pancreatica (*v. pancr.*) and the vena cephalica (*v. ceph.*) open into the posterior (dorsal) sac of the hepatic vein in *Desmoteuthis*. The vena cephalica accompanies the esophagus. Sections of a young *Cranchia* show that it may envelop the esophagus like a sinus, particularly at the point where the vein forms an ampulla (Plate L, Figure 7; Plate LIV, Figure 18, *amp. v.*) before it leaves the esophagus. In *Desmoteuthis* the vena cephalica forms a loop before it enters the sac of the hepatic vein; the loop was markedly inflated due to a hemorrhage (Plate LIV, Figures 12, 15, *v. ceph.*). Before it enters the venous sac, the vena cephalica receives the vena dorsalis (*v. dors.*) which extends from the median side of the mantle, together with the arteria dorsalis. The vena dorsalis, too, was not previously described.

The large single sac of the vena gastrica (Plate LIV, Figure 15, *sacc. v. g. g.*) opens posteriorly (dorsally) and is situated on the right side of the mid-intestine. The vena gastrica extends near the arteria gastrica and originates in the cord of connective tissue (*lig. g. g.*) which extends from the stomach to the posterior end of the body; it then branches on the stomach, receives a venous branch from the caecum and extends ventrally on the ductus hepato-pancreaticus to form the large sac.

From the confluence of all these sacs, which unite posterior to the liver, originate the large branchial arteries (*a. branch.*), which frequently still retain venous sacs. Into these arteries open the venae cordis which are almost symmetrical and branch on the heart. These veins have not been shown previously. I have a good preparation of these vessels in *Desmoteuthis* (Plate LIV, Figure 14, *v. cord.*).

The above-described arrangement of the venous sacs is more or less distinct in all genera of Cranchiidae. The sacs are weakly developed in *Bathothauma*, in which there is only a short dorsal
323 (posterior) sac of the vena hepatica and slight venous swellings at the bifurcation of the branchial arteries (Plate LVII, Figure 2, *sacc. ven.*).

The branchial arteries (*a. branch.*) which extend from the venous sacs are more strongly developed in the Cranchiidae than in other families of Cephalopoda. If the gills are widely separated, the branchial arteries are thick vessels which pass in an anterior curve to the branchial hearts (*Cranchia*, Plate L, Figure 6, *a. branch.*). This anterior curve is especially distinct in forms in which the gills are situated close together. Before their entrance into the branchial hearts, the branchial arteries bear venous appendages (Plate LVII, Figure 7, *sacc. ven.*) which are absent only in *Cranchia*. The appendages usually surround the distal end of the gills but they sometimes form large sacs, particularly in *Bathothauma* whose sacs replace the small median sacs (Plate LVII, Figure 2, *sacc. ven.*).

The vena pallialis, too, may bear venous sacs before its entrance into the branchial heart or into the end of the branchial arteries. This vein passes from the mantle on the suspensory ligament of the gill and then dorsal to the branchial heart.

The last to unite with the branchial arteries are the abdominal veins. They, too, bear terminal venous appendages—except in *Cranchia*—and open together with the above vessels into the branchial heart. In *Cranchia* there is a distinct horizontal branch which carries blood from the middle of the abdominal wall to the end of the abdominal vein.

The branchial hearts (*c. branch.*) are moderately large, usually oval or rounded. The arteriae branchiales extend from them to the base of the gills. The appendage of the branchial heart is not visible

from the ventral side; it is visible as a small appendage on the dorsal side of the branchial heart if the vessels at the base of the gill are cut and the branchial heart is folded back.

The venae branchiales, which carry arterial blood from the gills, pass dorsal to the branchial arteries. They are usually, but not always, swollen before they open into the thin-walled atria of the heart.

Body cavity

The structural conditions characteristic for the Cranchiidae are reflected also in the extremely large size of the body cavity, which consists of two parts that broadly communicate with each other, an anterior and a posterior part. The anterior part continues to the head where it is narrowed to a lateral slit by the brain and static organs. The division of the body cavity is most marked in *Bathothauma*, in which the visceral sac and thus also the body cavity are constricted behind the liver and the heart. Here, too, the passage between the anterior and posterior parts is narrowed to a slit which forms the border between the two parts behind the branchial hearts.

324 The anterior part of the body cavity in all Cranchiidae is divided by a median septum into a left and a right half (Plate L, Figure 7). This septum is attached along the gladius, passes to the vena cava and serves also as a suspensorium for the esophagus and the aorta cephalica which pass obliquely from the dorsal margin of the liver to the head. The septum is attached on the dorsal anterior margin of the liver and is bordered by the dorsal artery and vein toward the gladius. The septum covers the lateral parts of the liver in the form of two lamellae which extend to the dorsum and are surrounded posteriorly by silky muscular cords (*diaphr.*). The middle part of the body cavity has thus the form of a roof the top of which is formed by the dorsal artery and the sides by the free-hanging lamellae. These lamellae are best developed in *Cranchia* and *Desmoteuthis*, in which the silky muscular cords at the margin of the lamellae are distinct.

Renal sac

As in all the Oegopsida, the renal sacs of the Cranchiidae are fused in the middle, and no septum indicates their development from two separate sacs. However, the symmetrical position of the opening indicates that they developed by fusion of what originally were two separate sacs. The large renal sac lies posterior to the liver, surrounds its dorsal half anteriorly, and extends laterally to the branchial hearts. As the branchial hearts are widely separated, the lateral processes of the renal sac extend unusually far along the large branchial vessels. The dorsal anterior wall of the renal sac borders on the heart, on the venous sacs and on the large branchial vessels, and the ventral wall adheres to the thin abdominal wall. The renal sac is usually filled with a whitish coagulate which has to be removed to show the openings. The outer openings of the renal sac (*ur.*) lie symmetrically at the level of the posterior side of the liver or the venous sacs. In *Cranchia* and *Bathothauma* they are chimney-shaped, while in *Desmoteuthis* and *Owenia* these openings are oval and circled by a swollen margin. The inner openings, which on careful preparation become very clearly visible, lie diagonally anterior to the outer ones (Plate LVII, Figure 2, *d.coel.*). They lead into long tubes which continue trumpet-like widened from the anterior body cavities and pass obliquely toward the middle, approaching the outer openings on the ventral wall of the renal sac.

Genital organs

Having had no mature males at my disposal, I can give only a partial description of the genital conditions in the Cranchiidae. We collected a gigantic male of *Cranchia scabra*, but the genitals were surprisingly little developed. This is the case also in the other species of Cranchiidae, which is the reason why nothing is known so far on the spermatophores.

325 The genitalia of the females are better known, because Rathke studied a mature *Leachia* and I could confirm his data on this species. As already mentioned, Joubin recorded that the spawned-out females of *Leachia* appear in an exhausted condition on the surface where they are caught sometimes in large numbers, while the males have remained unknown. Some Cranchiidae probably grow very large before they become mature. This is suggested by the discovery of the large *Cranchia scabra* and by the fact that a relatively large female of *Bathothauma* had scarcely developed oviducts.

The genital glands are situated on the dorsal surface of the stomach, sometimes slightly to the right. From them extends the ligament, which tapers rapidly to a thread and enters into the cone of the gladius. A peculiarity of the genital gland of *Bathothauma* is that it is situated between the 2nd and 3rd (sac-shaped) part of the stomach, far from the ligament. The horseshoe-like curvature of the genital gland of *Bathothauma* is apparently caused by the fact that the terminal part of the stomach is secondarily curved anteriorly and is attached to the ligament near its apex.

The **male gonoducts** are described after a large specimen of *Cranchia*, in which they are relatively well developed (Plate L, Figures 15, 16). Opening of the mantle cavity showed the small, curved efferent duct of the spermatophore sac (*pen.*) near the base of the left gill; the appendage (*app. prost.*) projects near it as a small knob (Plate XLIX, Figure 8). There are no other differences from the conditions typical for the Oegopsida.

Examination of the "anlage" from the dorsal side (Figure 16) shows the ampulla-shaped opening (*amp.*) of the looped sperm duct (*v. def.*) at a large distance from the testis. The sperm duct extends anteriorly and opens into the first part of the vesicula seminalis (spermatophore gland) (*ves. sem. 1*). The other two parts are visible from the ventral side (Figure 15): the recurved 2nd part is divided into compartments (*ves. sem. 2*), the cylindrical 3rd part (*ves. sem. 3*) is curved anteriorly. The so-called prostate (*prost.*) is situated on the dorsal side; its appendage (*app. prost.*) forms a simple loop. The vas efferens and Needham's sac (Figure 16, *b. sperm.*) are still very short; only its anterior part (*pen.*), which projects freely into the mantle cavity with its recurved, club-shaped apex, is better developed.

The entire "anlage" is enclosed in a pocket (*sacc.*) the outer opening of which I could not locate.

The gonoducts of a large male *Liocranchia* were in an even more retarded condition, but otherwise resembled those of *Cranchia*. The male gonoducts of the other specimens were so small that it needed great care to locate them behind (dorsal to) the left branchial heart and make a preparation.

The **female gonoducts** are situated on both sides behind the branchial hearts and at the base of the gills. They have already been described by Rathke from a fully developed specimen of *Leachia*. They consist of two large, spirally coiled oviducts which bear a well-developed oviduct gland at the
326 opening (Plate LII, Figure 4, *gl. od.*). All authors, including Brock and Lönnberg, erroneously considered the oviduct gland as the anterior nidamental gland. In my specimen of *L. eschscholtzii*, this gland was folded together on the left side but was broadly open on the right. The inner surface of the oviduct gland is covered with numerous parallel glandular lamellae which had apparently been fully active in this specimen. If the preparation had not shown the connection with the oviduct, this structure could have been considered as an anterior pair of nidamental glands, the more so as the latter closely resemble the oviduct glands.

The **nidamental glands** (*nid.*) are distinguished by their large size. They resemble the cotyledons of higher plants which are just beginning to open. The inner surface of the glands, which is situated perpendicular to the surface of the body, is covered with regular parallel glandular lamellae. The two halves are rounded and fused posteriorly; they are covered with a thin, pigmented membrane. The gaping of the two halves is apparently due to the fact that this membrane tears anteriorly while the margin of the diverging halves is folded back in the form of a chamois horn. This was particularly distinct in a specimen of *Euzygaena*, in which the moderately developed nidamental glands showed a tear of the envelope and the recurved, free ends. The secretion of the nidamental glands is probably discharged by the opening of the mature glands in all Oegopsida, although in no other family do these glands open at such an early stage of sexual development as in the Cranchiidae.

In the other females examined, both gonoducts were in a very early state of development. In a medium-sized female of *Cranchia* (Plate L, Figure 6), the end part of the oviducts (*ovd.*), which later develops into the oviduct gland, was distinctly visible from the ventral side; it lies anterior to the branchial hearts; the narrow "anlagen" of the nidamental glands (*nid.*) were situated slightly inward, at the end of the long branchial arteries.

Hectocotylization

Hectocotylization of a ventral arm in the Cranchiidae was first observed by Lönnberg (1896, p. 610) in *Liocranchia reinhardtii.* He states that the left ventral arm is hectocotylized and that the small, densely arranged biserial suckers pass into wide papillae at the apex. I can confirm his data for a new species of *Liocranchia* which I named *L. valdiviae.* Examination of 3 specimens of this species showed that the left ventral arm is hectocotylized (Plate LI, Figures 8, 9, *hect.*). In the large male with retarded gonoducts, the left ventral arm is slightly shorter than the right. Its keel (swimming membrane) is slightly
327 better developed prior to the recurved tip and shows distinct differences in the formation of the suckers. The 4 pairs of proximal suckers are followed by 12 suckers in a row which become gradually smaller toward the tip. Younger specimens show a similar condition, but the last 3 pairs of suckers form 2 rows. The broad papillae described by Lönnberg were not present in this species.

I found that hectocotylization affects the right, not the left ventral arm in 2 other Cranchiidae. The specimen of *Cranchia scabra* has a well-developed hectocotylus (Plate L, Figures 1, 3, *hect.*) despite the retarded condition of the male gonoduct. The right ventral arm is shorter than the left one; it is thick, and its tip is bent dorsally at a right angle. The large keel (swimming membrane) is displaced dorsally and extends broadly around the tentacles to the 3rd arm. A few proximal suckers are biserial; these are followed by suckers in 3 rows and then by small suckers in 4 rows, followed, again, by a few pairs of biserial and, at the tip, irregularly arranged, small suckers. Hectocotylization affects also the 3rd arms, which bear numerous, densely arranged suckers at the tip.

In *Euzygaena*, too, I found the right ventral arm hectocotylized (Plate LII, Figure 3). It is considerably larger than the left one and bears densely arranged biserial suckers.

These observations on the hectocotylization suggest that the Cranchiidae resemble in this respect some species of Enoploteuthidae in which the transformation of one or several arms into a hectocotylus takes place at a very early stage, long before maturation of the genitalia. A correlation with approaching sexual maturity could not be demonstrated: both males of *Cranchia* and *Liocranchia* had very retarded gonads and gonoducts, despite the presence of fully developed hectocotyli. The only development relatable is that of the differentiation of the genitalia, which apparently takes place already in larval life—as we attempted to prove in several cases—i.e., it preceeds the transformation of the arms.

328 # *Cranchia*

Cranchia scabra Leach
(Plate XLVIII, Figures 1, 2; Plates XLIX, L, LX, Figures 1–6)

Cranchia scabra Leach, 1817, *"Tuckey" Exped. to Zaire*, Append., p. 410, Plate XVIII, Figure 1; *Zool. Misc.*, Vol. III, p. 140.
Philonexis eylais d'Orbigny, 1835, *Voy. Amér. mérid. Moll.*, p. 20, Plate I, Figures 8–14.
Cranchia scabra Owen, 1836, "New and Rare Ceph.", *Trans. Zool. Soc.*, Vol. II, p. 103, Plate 21, Figures 1–5.
Philonexis eylais Férussac and d'Orbigny, 1835–48, *Céph. acét.*, p. 102, *Octopus*, Plate XVII, Figures 4, 5.
Cranchia scabra Férussac and d'Orbigny, 1835–48, *Céph. acét.*, p. 22, *Cranchia*, Plate I, Figure 1.
Cranchia scabra Gray, 1849, *Cat. Moll. Brit. Mus.*, p. 38.
Cranchia scabra Steenstrup, 1861, *Overblik, Cranchiaeformes*, p. 72.
Cranchia hispida Pfeffer, 1884, *Ceph. Hamb. Mus.*, p. 27, Plate III, Figure 36.
Cranchia tenuitentaculata Pfeffer, 1884, *ibid.*, p. 26, Plate III, Figure 37.
Cranchia scabra Hoyle, 1886, *Ceph. "Challenger" Exp.*, p. 44.
Cranchia scabra Jatta, 1889, "Cef. 'Vettor Pisani'", *Boll. Soc. Nat. Napoli*, p. 67.
Cranchia scabra Pfeffer, 1900, *Syn. Oeg. Ceph.*, p. 195.
Cranchia scabra Hoyle, 1904, *Rep. "Albatross" Ceph.*, p. 43, Plate X, Figure 11.
Cranchia scabra Chun, 1906, *Syst. d. Cranchien*, p. 84.

Locality: Station 49: South Equatorial Current, 0°20′ N, 6°45′ W. Vertical net to 3,500 m—One large male.
Station 217: Indian North Equatorial Current, 4°56′ N, 78°,5′ E. Vertical net to 2,000 m—One medium-sized specimen.

On 8 September 1898, we collected a fascinating specimen of *Cranchia scabra* in a vertical net to a depth of 3,500 m in the South Equatorial Current. It was in excellent shape and very large—a giant compared to other specimens of *Cranchia.* We kept it alove for 2 hours in iced seawater, for photography and drawing. Plate XLVIII shows the habitus of this specimen, drawn after the photographs and the sketches. It reveals that the plump, balloonlike form of the body is being caused by preservation and does not show the natural condition. The live animal has a spindle-shaped body which tapers slightly toward the mantle margin and has a pointed posterior end. The ratio between length of mantle and dorsoventral axis in lateral view is 1 : 1,8 (i.e. nearly 1 : 2). This corresponds to the resting state of the uncontracted mantle. During contraction, the mantle becomes slightly inflated, as I repeatedly observed in the smaller specimen from the Indian Ocean. During preservation, head and eyes are retracted almost completely into the mantle cavity, to the base of the arms. The anterior margin of the mantle of the live animal is
329 situated more or less at the level of the posterior margin of the eye, although the head may sometimes protrude farter. The mantle corners do not project, due to their fusion with the body; rather, they look as if they were retracted, because of the retraction of the head in preserved specimens.

The **mantle** is rugose because it has a dense, irregular cover of cartilaginous tubercles which vary in size; larger tubercles are situated between smaller and medium-sized tubercles. The head and arms do not have such tubercles, but on the outer side of the fins, excepting the margin, they are present. The margin of mantle and fins usually bears only very small tubercles, but such tubercles may also be present on other parts of the body. The tubercles are sometimes arranged in curves, but there is no regular pattern. They appear early and afford an excellent character for the identification of the youngest larvae of *Cranchia.* They form thick pillars with 4 short branches, each ending in 4 or 5 spines (Plate XLIX, Figure 4). Pfeffer names them chitinous tubercles, but this is incorrect since histological examination shows that they consist of cartilage with embedded cells.

The so-called chitinous ridges of the mantle, which extend from the ventral corners on the funnel, are also cartilaginous. They diverge at an angle of about 60°, while the adjacent submedian ridges are almost parallel. The ridges strengthen the margins of fusion of the funnel, the ventral margins of the collaris and the lateral margins of the depressor infundibuli.

The fins form a nearly oblong oval. Compared to the mantle they are relatively small, even in the large specimen; the dorsal length of the mantle (gladius) is 82 mm, that of the fins 18 mm, so that the ratio is 4.5 : 1. The fins project 9 mm behind the posterior end of the body where they are fused into a lamella having a heart-shaped indentation; their dorsal bases diverge at an angle of 70° along the spoon-shaped end of the gladius. In young specimens the fins are separated and only in specimens of medium size a median posterior union is weakly indicated (Plate XLIX, Figure 5).

The **head** is short and thick, having a slightly conical anterior part. It consists mainly of the large eyes, 14 mm wide, which are sessile, i.e. invaginated in the head. The eyeballs of the live animal are blackish violet. The iris has a silvery sheen with metallic green and red reflection. In the preserved specimen the eyes were half retracted into the mantle and the lid fold covered them completely; the opening of the lid was closed by the rampart-like contracted margins (Plate L, Figure 3). Examination showed a weakly indicated presence of gelatinous tissue in the cutis of the head and base of the arms.

Luminous organs are present on the eyeball; they are described below. The short, knob-shaped olfactory tubercle is situated near the ventral margin of the eye. It is flattened, measures 1 mm and has a broad base (Plate L, Figure 4, *tub. olf.*).

330 The **funnel** is moderately large. In life it extends to the level of the anterior margin of the eye. In the preserved specimen its opening hangs flaccidly down. A funnel valve is absent. The funnel organ unfortunately had folded due to strong contraction during preservation, so that its form could not be determined. The single dorsal lobe forms a broad band with a tongue-shaped process in the middle, while the paired parts are large and oval.

Arm Apparatus

The arms of *Cranchia* are more strongly developed than those of other genera of the family (Plate L, Figure 1). The arm formula is 3, 2, 4, 1. All arms bear large biserial suckers, excepting some cases which will be mentioned below. These suckers are usually larger in the middle of the arm and smaller distally; they have smooth, undenticulate rings, only a few large rings showing some slight identations on the margin in the distal part.

All arms have large protective membranes supported by muscular bridges which alternate regularly with the suckers. The protective membranes in the neighborhood of the 1st and 2nd arms widen at the base into a rudimentary sail-like membrane, as illustrated by Owen. Another sail-like membrane, formed by the outer membranes (*lam. ext.*) extends between the 2nd and 3rd arms. The swimming membranes on the 1st and 2nd arms are only weakly indicated; on the 3rd arms, however, they form distinct keels from the base to the tip. On the right 4th arm, the swimming membrane is unusually well developed and toward the base it forms a wide web which surrounds the tentacle and extends toward the 3rd arm but does not pass into the swimming membrane of the latter (Plate L, Figure 3). The swimming membrane of the left 4th arm is less well-developed, although it surrounds the left tentacle at the base as broadly as that of the right arm.

The **tentacles** are relatively short, thick, with a markedly widened club. The stalk of the tentacle has a flat inner surface with a weak median groove. In the distal part, the stalk bears to the right 13,

to the left 15 pairs of small suckers at regular intervals, which alternate in a zigzag pattern. Between the suckers are delicate adhesive knobs, some of which are recognizable only under good illumination. The club is 8 mm long and its tip is bent dorsally in the form of a chamois horn. The protective membranes of the club are strongly developed and have distinct muscular bridges; also present is a sharp keel, which is displaced dorsally at the tip (Plate L, Figure 2). The suckers are arranged in 22 quadriserial rows; they are largest in the middle of the club and become gradually smaller toward the tip. There is a kind of carpal part which is distinguished by adhesive knobs between the last quadriserial rows of suckers at the boundary with the stalk; I found 5 to 6 knobs in this part.

331 PFEFFER stated that the suckers on the tentacles have "rudimentary rings which are not quite smooth." I found that the well-developed chitinous rings bear about 20 denticles at regular intervals which become smaller proximally. About 9 or 10 yellowish brown denticles, shiny like silk, distinctly project.

The **attachment** shows the normal condition in the Cranchiidae. There are 7 buccal pillars, of which the two ventral ones are situated close together. The 1st and 2nd arms are attached dorsally, the 3rd and 4th arms ventrally. The buccal membrane is not very high, has a wrinkled inner side, and the outer and inner lips show distinct fluting.

Hectocotylization

The 3rd and 4th arms of the large specimen—which proved to be a male—show characters of hectocotylization and are therefore described in detail.

The modification of the 3rd arms consists in the arrangement of the suckers at the tip; its normal biserial arrangement is replaced by an arrangement in 4 or many rows (Plate L, Figure 1). The arms have a large swimming membrane which extends to the tip and does not pass into the outer membrane between the 2nd and 3rd arms. Their protective membrane are as large as those of the 1st and 2nd arms; they gradually taper toward the base. There are 23 biserial suckers on the left 3rd arms, followed rather suddenly at the tip by a few rows of 4 suckers and then numerous densely arranged small suckers which show at first an arrangement in oblique rows of 6 to 7 suckers and then irrregularly arranged suckers.

That this represents hectocotylization is proved by comparison with the formation of the 3rd arms of the female. The largest female, with a dorsal mantle length of 49 mm, has at the tip of the arm tiny biserial suckers, following rather abruptly after the larger suckers.

The right ventral arm is transformed into a fully developed **hectocotylus.** It is thick, 12 mm long and its tip is curved dorsally at a right angle. It is distinguished by a strong swimming membrane which, too, is displaced dorsally, passes broadly at the base around the tentacle and extends to the 3rd arm (Figure 3). The protective membranes have dense muscular bridges and are much more slender than those on the other arms. The suckers show a very characteristic arrangement: two biserial proximal pairs are followed by 5 rows of 3 suckers and finally by a larger number of rows of 4 suckers. There are thus 24 rows of suckers which are arranged more or less regularly to the dorsal curvature of the apex. Here follow at first 5 pairs of larger biserial suckers, then two quadriserial rows of suckers, and finally dense, irregularly arranged small suckers.

332 The left ventral arm is of normal form and bears about 30 biserial pairs of suckers to the tip. It is slender, 17 mm long, and thus longer than the hectocotylus.

The **gladius** (Plate XLIX, Figures 9, 10) is distinctly visible. The gladius of *Cranchia* has never been described in detail and I therefore made a preparation of the gladius of a female. It is 48 mm long and does not differ much from that of the large male. Its anterior part is formed almost entirely by the rhachis and shows a very simple structure; it consists of a narrow chitinous lamella which is nearly sickle-shaped in cross section. Posteriorly it widens and has a sharp keel on the median outer surface. The flat lateral margins, which correspond to the vane, are curved ventrally and form a short, wide, flat terminal cone. The gladius of the large male is 82 mm long; its maximal width is 8 mm at the anterior margin of the fins.

The **coloration** of the large specimen shows a brownish, slightly pink key tone which is caused by the numerous chromatophores scattered irregularly on the mantle and arms. The chromatophores on the arms are not arranged in distinct rows, either. The chromatophores on the club, on the other hand, form 4 longitudinal rows with irregularly arranged chromatophores between them. Particularly large and vividly colored chromatophores are situated on the base of the tentacles and ventral arms near the funnel.

Luminous Organs
(Plate L, Figures 4, 5)

Pfeffer (1900, p. 195) stated that "a crest with several luminous tubercles is present on the margin of the eye." As nothing has been published on the number, size and arrangement of the luminous organs, the following is of interest: *Cranchia scabra* has 13 luminous organs, all except two on the ventral surface of the eyeball. The ventral organs are arranged in two more or less concentric circles. The outer circle consists of 7 organs (1 . . . 7); it surrounds the anterior and inner margin of the eyeball, beginning from the base of the 3rd arm. These organs are widely seperated, but their padlike, golden layers are almost contiguous so that they form what appears to be a continuous crest. The inner circle consists of 4 organs (8 . . . 11) and is situated in about the middle between the margin of the iris and the outer circle. There are also 2 small organs, situated dorsal to the margin of the iris (12, 13).

The organs are whitish in the preserved specimen and are oblong or oval. They always have a
333 narrow slit which may be straight or curved. The organs of the large male measure 1 mm, those of the smaller specimen (Figure 5) 0.5 to 0.8 mm. The 4 organs of the inner circle are slightly larger than those of the outer circle. All organs are surrounded by a delicate pad which extends like a mirror in the form of a wedge toward the lens in the 7 organs of the outer circle.

The position of the organs with respect to the adjacent parts of the head is shown in Figure 4, which shows their topography in the large male of *Cranchia scabra* after removal of the eyelid. The organs Nos. 5, 6 and 7 are situated on the anterior margin of the eyeball, at the level of the base of the 4th, 3rd and 2nd arms. The other 5 organs of the outer row are situated on the ventral inner margin of the eyeball, of these, organs Nos. 2 and 3 just before the knoblike olfactory tubercle. The 4 organs of the inner circle are more widely spaced in the larger specimen. Also shown in the drawing is the dorsal position of the small organs 12 and 13 above the iris.

The fine structure of the organs will be described in connection with the similar organs of *Liocranchia.*

Mantle Complex
(Plate XLIX, Figures 7, 8)

Opening of the large mantle cavity shows the characteristic width of the visceral sac. This applies also to the large male the mantle cavity of which is shown in Figure 7. The width of the visceral sac is not a result of the large size of the inner organs but is caused mainly by the unusually large body cavity. The paired anterior parts of the body cavity communicate broadly with the single posterior part, through which the stomach and caecum are partly visible together with the afferent and efferent parts of the intestinal tract.

Characteristic for the genus Cranchia is also the large distance between the gills. The male has large compact gills which are 13 mm long. The long afferent and efferent vessels which are distinctly visible near the branchial hearts are correspondingly long. The musculus depressor infundibuli (*mu. depr. inf.*) of this species forms a broad lamella which is fused with the mantle, curves around the gill, extends into the posterior wall of the funnel and then is contiguous with the anterior part of the visceral sac. As the gills are suspended on long branchial ligaments (*susp. branch.*) the dorsal insertion of which on the mantle almost completely closes the two dorsal mantle sacs posteriorly, the respiratory water passes through the spiracula over the gills (see p. 9) and enters the large ventral mantle cavity. In contrast to the other Oegopsida, a broad median septum is lacking. However, it is not completely absent but is reduced to a small triangular lamella (*sept.*) situated at the posterior end of the body. At its anterior margin passes the arteria pallialis which branches from the arteria posterior situated on the visceral sac. The figure also shows the entrance into the funnel as revealed by the
334 opening of the mantle cavity of the strongly contracted specimen. The ventral wall of the funnel (*m. inf. ventr.*), which is shown to be folded upward, is attached to the corresponding submedian cartilaginous stripes of the mantle. The dorsal wall of the funnel passes into the musculus depressor infundibuli. The median funnel organ is strongly shrunken and has a small, lanceolate, tongue-shaped process in the middle. The liver projects near the rectum with the two anal appendages. The suspensory ligament extends toward the liver and anus as a sharp ridge. On both sides of the liver, at about the level of its posterior margin, are situated the outer openings of the renal sac which form oval papillae with a slit. Also visible are the inner openings of the renal sacs into the body cavity.

The vena cava passes on the ventral surface, just posterior to the funnel organ, in an undulate course caused by preservation. It then forms a broad curve around the liver. In addition to the thick, long branchial vessels mentioned above (Figure 8, *a. branch.*, *v. branch.*) and the oval branchial hearts (*c. branch.*) there are the two large abdominal veins at the sides (*v. abd.*); also visible is the thin arteria posterior which passes on the median ventral side.

The genitalia are much more retarded than would be expected in view of the marked hectocotylization. The specimen is a male and the opening of the spermatophore sac, which is directed posteriorly, is visible above the base of the left gill and the branchial heart (Figure 8, *pen.*); also visible nearby is the small, knoblike appendage of the gonoduct (*app. prost.*). The testis is situated at the posterior end of the body, far from the efferent ducts, and is visible as a whitish body which borders on the stomach.

Inner Organs

The inner organization of *Cranchia scabra* has already been described in detail in the general review of the Cranchiidae, especially the intestinal tract and its glands (p. 248). The following description deals therefore only with a few organs of particular interest.

Vascular System

Arterial circulation. The heart of *Cranchia scabra* (Plate L, Figures 6, 7) is spindle-shaped and tapers slightly at the exit of the large aorta cephalica. It is situated on the right side behind the liver, displacing the two hepatic ducts to the left. At its ventral apex originates the arteria posterior (*a. post.*), whose course was already discussed in connection with the mantle cavity. The aorta cephalica
335 (*a. ceph.*) which originates at the dorsal apex of the heart, is slightly swollen at the base. It branches dorsal to the right hepatic duct into the arteria hepatica (*a. hep.*), which begins at the same level, and the arteria dorsalis (*a. dors.*), which borders on the ridge of the median septum. The aorta then passes along the esophagus and bifurcates behind the cerebal ganglion (Figure 9). The aorta has a thick envelope and is embedded in a cord of connective tissue which also surrounds the esophagus and is attached to the median septum. In this cord extend longitudinal muscles which are especially strongly developed near the aorta.

Venous circulation. The vena cava (*v. c.*) appears on the abdominal wall behind the median funnel organ and passes in the middle to the liver, which it surrounds on the right side. The vena cava becomes dilated into a venous sac behind the liver (Figures 7, 14) which receives the two long sacs of the hepatic veins (*sacc. v. hep. ant.* and *post.*), one of them from behind (dorsally), the other frontally (ventrally); these 3 sacs are connected on the dorsal side with the broad median sac of the vena gastrica (Figure 14, *v. g. g.*). It also receives the vena cephalica, which accompanies the esophagus and the vena dorsalis which opens in the vena cephalica (Figure 7, *v. dors.*). The vena cephalica partly envelops the esophagus and is broadly sickle-shaped in cross section. Before it leaves the esophagus and opens into the venous sac, the vena cephalica forms an ampulla (*amp. v.*) which completely surrounds the esophagus as a venous sinus, as shown in cross section.

After the union of all these venous sacs, the vena cava branches into two large branchial arteries (*a. branch*). They extend in an anteriorly convex curve and are very long, which is commensurate with the large distance between the two gills; they open directly into the oval branchial hearts (*c. branch.*), without first forming venous dilatations. Before they enter the branchial hearts, the branchial arteries receive the vena abdominalis (Figure 6, *v. abd.*) which extends from the posterior side, and the vena pallialis (*v. pall.*), which passes partly on the suspensorium of the gills. There is a lateral vein in the large male (Plate XLIX, Figure 8, *v. lat.*) which carries blood from the abdominal wall to the abdominal vein before it enters the branchial heart.

The branchial veins (*v. branch.*) are more weakly developed than the large branchial arteries; they pass dorsal to the latter and nearly parallel to them and then enter the heart, having slightly widened to constitute atria.

The **body cavity** of *Cranchia* is unusually large. The posterior part of the body cavity passes dorsal to the large branchial vessels into the paired anterior parts. The division into two anterior sacs of the body cavity is caused by a broad diaphragm (Plate L, Figure 7) which extends dorsoventrally from the gladius to the vena cava and is bordered posteriorly by the arteria dorsalis. The diaphragm is divided near the liver into two roof-shaped lamellae (*diaphr.*) which cover the liver and the adjacent vessels in lateral view. The free margin of the lamellae projects into the single posterior body cavity
336 and bears strong muscular cords. These cords have a silky sheen in the large male of *Cranchia scabra* and extend dorsally to the gladius.

Sections of the diaphragm show weak longitudinal muscles extending through its middle; muscular cords pass dorsoventrally on top of these muscles, to both sides.

The **renal sac** shows the normal conditions and opens into two oval renal papillae (Plate L, Figure 6, *ur.*) at the level of the posterior margin of the liver. These papillae are distinctly visible upon opening of the mantle cavity of the large specimen (Plate XLIX, Figure 7). The trumpet-shaped inner openings of the renal sac are also visible, because of the transparency of the abdominal wall to which they extend obliquely. The renal sac of *Cranchia* should be very wide, because it extends to the branchial hearts; I did, however, not examine these conditions in the large specimen, so as not to damage it.

The **genital conditions** have already been described in the general part (p. 255). The testis of the large male borders on the dorsal side of the stomach (Plate L, Figure 13, *test.*) and is 5 mm long. The large, groove-shaped gastrogenital ligament is visible at the posterior end of the testis (*lig. g. g*).

Measurements of the Male from Station 49

Dorsal length of mantle (length of gladius)	82 mm
Maximal width of gladius between fins	8 mm
Length of fins	18 mm
Width of one fin	14 mm
Width of head	23 mm
Width of eye	14 mm
Length of 1st arm	10 mm
Length of 2nd arm	19 mm
Length of 3rd arm	25 mm
Length of left 4th arm	17 mm
Length of hectocotylus	12 mm
Length of tentacle	40 mm
Length of club	8 mm

Liocranchia Pfeffer, 1884

Liocranchia reinhardtii Steenstrup
(Plate LI, Figures 5, 6, 7)

Leachia reinhardtii Steenstrup, 1856, "Hectocotylidannelsen," *D. Vid. Selsk. Skr.*, 5, R. IV, p. 200 (16).

Cranchia reinhardtii Steenstrup, 1861, *Cranchiaeformes*, p. 8.

Cranchia reinhardtii Brock, 1883, "Anat. Syst. Ceph.," *Z. w. Zool.*, Vol. XXXVI, p. 605, Plate XXXVII, Figure 4.

Liocranchia brockii Pfeffer, 1884, *Ceph. Hamb. Mus.*, p. 25, Plate III, Figures 33, 33a.

Liocranchia reinhardtii Pfeffer, 1884, *ibid.*, Figure 35.

Cranchia (*Liocranchia*) *reinhardtii* Hoyle, 1886, "*Challenger*" *Ceph.*, p. 184; Plate XXXI, Figures 11–14, Plate XXXII, Figures 1–4.

Cranchia reinhardti Lönnberg, 1896, *Rare Ceph.*, p. 609, Figures 1–4.

Liocranchia reinhardti Pfeffer, 1900, *Syn. Oeg. Ceph.*, p. 194.

Liocranchia reinhardtii Chun, 1906, *Syst. d. Cranchien*, p. 84.

Liocranchia elongata Issel, 1908, *Cef. "Liguria,"* p. 220, Plate X, Figures 28–32.

Cranchia (*Liocranchia*) *globula* Berry, 1909, *Hawaiian Ceph.*, p. 415, Figure 9.

337 **Locality:** Station 54: Guinea Current, 1°51′ N, 0°31′ E. Vertical net to 2,000 m—One specimen of 15 mm dorsal mantle length.

Station 64: Branch of the Benguela Current, 0°25′ N, 7°0′ E. Vertical net to 2,000 m—Two larvae of 9 and 7 mm dorsal mantle length.

Station 66: Branch of the Benguela Current, 3°55′ S, 7°48′ E. Vertical net to 200 m—One larva.

Station 215: Indian North Equatorial Current, 7°1′ N, 85°56′ E. Vertical net to 2,500 m—One larva of 9 mm dorsal mantle length.

Station 217: Indian North Equatorial Current, 4°56′ N, 78°15′ E. Vertical net to 2,000 m—One specimen of 12 mm dorsal mantle length.

Liocranchia reinhardtii is widely distributed. We now established its occurrence in the Indian Ocean, too. As the above measurements show, we collected only larvae of juveniles. Since these specimens give valuable information on the postembryonic development which, we hope, emphasizes the need for care in the establishment of new species, they will be described later, together with the juvenile forms of *Cranchia scabra*. Here I could only note that I consider the recently established species *L. elongata* Issel and *L. globula* Berry to be identical with *L. reinhardtii*. The descriptions of Issel and Berry do not give a single specific character which distinguishes the two species. Berry considers the spherical form of his specimens as a specific character. However, this form of the body is caused by the strong contraction of the mantle margin, which closes the funnel. I have repeatedly observed that the nearly spindle-shaped mantle of *Cranchia* and *Liocranchia* may become inflated into a sphere. Preservation often causes a spasmodic contraction of the mantle margin, so that the animals are inflated like a balloon by the time they die.

Liocranchia valdiviae Chun

(Plate XLVIII, Figures 3, 4; Plate LI, Figures 1–4, 8–14; Plate LX, Figures 7–11)

Liocranchia valdiviae Chun, 1906, p. 84.

Locality: Station 182: Indian South Equatorial Current, 10°8′ S, 97°14′ E. Vertical net to 2,400 m—One male of 22 mm dorsal mantle length.

Station 221: Indian Countercurrent, 4°5′ S, 23°24′ E. Vertical net to 2,000 m—One larva of 8 mm dorsal mantle length.

Station 226: Indian Countercurrent, 4°5′ S, 70°1′ E. Vertical net to 2,000 m—One very small larva of 3.5 mm dorsal mantle length.

Station 237: Branch of the Indian South Equatorial Current, 4°45′ S, 48°58′ E. Vertical net to 2,000 m—One female.

338 Station 239: Branch of the Indian South Equatorial Current, 5°42′ S, 43°36′ E. Vertical net to 2,500 m—One male of 25 mm dorsal mantle length.

Station 258: Indian North Equatorial Current, 2°58′ N, 46°50′ E. Trawl, 1,362 m—One male of 40 mm dorsal mantle length.

The slender, goblet-shaped body has a narrow posterior end, beyond which project the relatively large fins. The head is short, broad, with protruding eyes. The arms are moderately long; the relatively thick tentacles are longer than the arms. The body is fleshy, partly transparent and has a relatively small number of chromatophores.

The **mantle** has a dorsal length of 40 mm and is about 15 mm wide in the largest specimen, a male from Station 258. The anterior margin of the mantle projects slightly at the points of fusion with the lateral margin of the funnel and in the dorsal line. From each ventral corner extend two cartilaginous ridges which diverge at an acute angle; in the preserved animal, their gray color contrasted with the mantle surface. The cartilaginous ridges bear conical, small and large, regularly alternating tubercles. On the mantle corners, where the cartilaginous ridges meet, are 3 tubercles; and further ventrally, a smaller 4th tubercle. The number of tubercles on the ridges is apparently very variable. In the above-mentioned larger specimen there are 15 tubercles on the right dorsal cartilaginous ridge and 17 on the right ventral ridge, only 13 on the dorsal, but 21 tubercles on the ventral ridges on the left side. In contrast to *L. reinhardtii*, there are no tubercles on the dorsal side along the gladius; however, the gladius is shining through unusually distinctly.

The **fins** are contiguous in the median line at their dorsal base and diverge anteriorly along the widened end of the gladius. Their musculature diverges also posteriorly, where a thin membrane connects the two fins. The fins project about 2.5 mm behind the posterior end of the body and have a nearly circular outline with a slightly heart-shaped incision at the posterior margin. They are 7.5 mm long and 9 mm wide.

The **funnel** extends to about the level of the anterior margin of the eyes, as is the case in most Cranchiidae. The funnel organ consists of two large oval lateral parts which are contiguous ventrally, and a three-pronged median dorsal part. The median funnel organ bears a short, protruding cone, rising just in front of the vena cava; there is also a cone-shaped tubercle on each of the lateral parts. A funnel valve is absent.

The **head** is characterized by large, protruding eyes. In the live animal, the eyeball shines gray-blue through the head; the iris has a silvery sheen. The eyeball is almost spherical; in young specimens,
339 however, it is more ellipsoid. On the ventral side, the eyeball bears an olfactory tubercle with a short stalk. Also situated on the eyeball are 4 large luminous organs (Plate LX, Figure 7, *phot.*). The anterior organ is situated at the base of the tentacle, the posterior below the olfactory tubercle. The organs appeared as silvery spots in the live animal; they are visible through the skin also in preserved specimens. The head is broad and short because of the protruding eyes and 10 mm wide in the largest specimen.

The **arm apparatus** (Plate LI, Figure 10) is moderately large; the formula is 3, 2, 4, 1. The 1st arms are 4.5 mm long in the large specimen; they are connected at the base by sail-like protective membranes. They bear 8 pairs of suckers of nearly the same size, only the suckers at the tip being slightly smaller.

The 2nd arms are 6.5 mm long and bear 12 pairs of suckers. They are of the same size from the base and become gradually smaller only at the tip; the last two pairs are very small.

The 3rd arms are 8.5 mm long. They bear 12–13 pairs of larger suckers, followed by about 7 pairs of very small suckers at the tip. They have a distinct swimming membrane (keel); these membranes are barely recognizable on the first 2 pairs of arms.

The first 3 pairs of arms have distinct protective membranes which are, however, not as wide as in *Cranchia. Liocranchia* resembles *Cranchia* also in that only the 1st and 2nd arms are connected by protective membranes, while the connection between the 2nd and 3rd arms is effected by the outer margins, though less distinctly than in *Cranchia.*

The 4th arms are of particular interest owing to the hectocotylization of the left ventral arm, which was first observed by LÖNNBERG. I am able to confirm this development for *L. valdiviae*, but found differences from *L. reinhardtii* in some details of the hectocotylization. According to LÖNNBERG, the

suckers of the hectocotylus are biserial and much smaller than on the right ventral arm; they pass gradually into broad papillae at the tip which differ distinctly from juvenile suckers.

The largest male of *L. valdiviae* (Station 258) has 14 pairs of suckers on the normal right ventral arm. These suckers become gradually smaller and are strictly biserial (Plate LI, Figure 9). A narrow swimming membrane extends to the tip of this arm.

The **left ventral arm is hectocotylized** and only slightly shorter than the right one. Its apex is much more strongly recurved than that of the right arm and bears a wider swimming membrane; the latter extends to the base of the arm. Only the 4 proximal pairs of suckers show the normal biserial arrangement. Then follow 12 suckers in one row which become gradually smaller; the 2nd sucker is slightly larger than the others.

340 Distinct characters of hectocotylization were found also in two smaller males.

A male of 25 mm mantle length (Station 239) bears 4 pairs of proximal suckers, followed by 7 uniserial suckers of gradually decreasing size and then 7 or 8 very small, irregularly arranged suckers at the tip (Plate LI, Figure 8).

A male smaller still, has a dorsal mantle length of 22 mm (Station 182) and 5 proximal pairs of suckers, then 8 uniserial suckers and 3 pairs of small suckers at the tip. The first of the uniserial suckers is larger than the preceding paired suckers. The hectocotylus is slightly larger than the right ventral arm.

Recapitulating the above-noted features of hectocotylization, we find that the usual biserial arrangement of suckers has disappeared in *L. valdiviae* except at the base of the hectocotylus, which bears 4 or 5 pairs. An indication of a biserial arrangement may also persist at the tip. In contrast to *L. reinhardtii*, however, the small outer suckers show no transformation into broad papillae either.

The **tentacles** (Plate LI, Figure 12) are relatively short and thick; they are 19 mm long in the largest specimen and have an only slightly widened club. The tentacle stalk is almost cylindrical at the base and becomes gradually flattened on the inner side. PFEFFER (1900, p. 190) considers the absence of suckers on the tentacle stalk as characteristic for the genus *Liocranchia*. This would be unique among the Cranchiidae. However, examination of both species of *Liocranchia* showed that suckers are, in fact, present on the tentacle stalk. True, in the largest specimen of *L. valdiviae* there are only 6 suckers, forming a long zigzag arrangement on the distal part of the stalk. A younger specimen of *L. reinhardtii*, however, bears more numerous suckers on the tentacle stalk, so that the absence of suckers on the stalk is definitely not a generic character.

The **club** is 5.5 mm long in the largest specimen of *L. valdiviae*. Its tip is slightly curved dorsally and bears a keel (swimming membrane) that has the form of a cockscomb. The protective membranes (Plate LI, Figure 11) have broad muscular supports. The ventral protective membrane is slightly wider than the dorsal one. The suckers on the club begin proximally with 2 or 3 pairs in 2 rows. They could be considered as a carpal part because there are 4–5 distinct adhesive knobs between them in the largest specimen. Then follow the usual rows of 4 suckers; those in the middle of the club are larger than the proximal and distal suckers.

The **buccal funnel** (Figure 10) is moderately high and shows 7 well-developed buccal pillars. The
341 attachments which extend from the pillars show the normal condition of *Cranchia*; the two dorsal pairs
of arms are attached dorsally, the other two pairs ventrally. The margin of the outer lip is sharp and smooth, that of the inner lip regularly fluted.

The **coloration** of *Liocranchia* is not very striking. The live specimens were semitransparent, with relatively weak pigmentation. A row of dorsal chromatophores along the gladius, diverging into two rows at its widened end, is the most conspicuous feature. Chromatophores are also present on the dorsal side; they are scattered, orange or reddish and do not show any distinct arrangement in transverse rows.

The fins have no chromatophores, except at the dorsal heart-shaped incision of the posterior margin. The dorsal side of the head is covered with symmetrically arranged chromatophores in young specimens. Two larger chromatophores are situated on each eye. Younger specimens have only 3 chromatophores at the posterior end on the ventral side. Sparse chromatophores are scattered over the whole ventral surface in older specimens. The outer side of the arms bear a row of larger chromatophores and there is one chromatophore behind each sucker on the inner side (Figure 9). The tentacles have a rather vividly pigmented outer side and the club has distinct, larger chromatophores in the middle. A few spots of pigment are also present on the inner side of the club behind the suckers.

Inner organs

(Plate LI, Figures 13, 14)

The inner anatomy of *Liocranchia* will be described briefly since it does not differ much from the typical condition of the Cranchiidae.

Intestinal Tract

The esophagus (*oes.*) opens in the initial part of the sac-shaped, strongly muscular stomach (*st.*), which contains large inner folds. The stomach opens broadly into the large, thin-walled caecum (*st. coec.*) and also into the mid-intestine (Figure 14). The caecum is almost as long as the stomach and bears spiral folds. They are only weakly developed, as in *Cranchia*, and pass into a groove (Figure 14, *sulc.*) bordered by two swellings. The groove also forms the anterior border of the large opening of the stomach; the posterior margin of this opening bears weak indentations.

The largest specimen of *Liocranchia* shows two important characters. One is the fact that the stomach and caecum are situated at the posterior end of the body at a large distance from the liver; the other is the peculiar condition of the 3 ducts which lead to the stomach and caecum, i.e. the esophageal, the mid-intestinal and the hepato-pancreatic ducts: these are so densely spirally coiled that it would be difficult to recognize them without comparing them with those of other Cranchiidae. There must have existed very peculiar one-sided thickenings of the walls, creating tensions which
342 finally resulted in the spiral coiling into about 20 windings (Figures 13, *spir.*). The liver, stomach and caecum are not affected by this coiling, which is proved by their normal position and by the fact that there is no coiling of the long, thin gastro-genital ligament (*lig. g. g.*), that originates on the stomach and bears the genital gland. The mid-intestine is not sharply delimited from the rectum, and the anal appendages are relatively small.

The position of the liver (*hep.*) is vertical, and its dorsal end is wider than the ventral one. The ducts which extend from it are densely covered with pancreatic appendages (*pancr.*), which are larger on the left than on the right. These appendages adhere closely to the liver and heart and open in the long ductus hepato-pancreaticus, which is wound in a spiral around esophagus and mid-intestine.

Vascular System

The vena cava (*v. c.*) ascends on the right side around the liver and opens in a large sac with dense venous appendages. The beginning of this sac receives on the right side the venous sacs of the hepatic veins—an anterior (*sacc. v. hep. a.*) and a posterior (*sacc. v. hep. p.*) sac. The branches of the vena cava which extend as branchial arteries (*a. branch.*) to the branchial hearts (*c. branch.*) are relatively short

because the bases of the gills are not as widely separated as in *Cranchia.* The branchial arteries also bear small venous appendages before they open into the branchial hearts.

The gills are well developed, although loosely built. They are 6 mm long and thus comprise only one-seventh of the mantle length. The thin-walled branchial veins (*v. branch.*) do not markedly widen into atria as they open into the oval heart. The large aorta cephalica (*a. ceph.*) originates on the right side of the heart.

The other systems of organs do not differ much from the normal condition and only the **male genitalia** will be briefly described. The testis (*test.*) is situated dorsally on the posterior end of the stomach, slightly to the left. It is oval and only 1.5 mm long. The penis (end of spermatophore sac) projects freely into the mantle cavity, dorsal to the base of the left gill. A small part of the appendage of the prostate is also shining through. The male genitalia are rather retarded, but the division of the vesicula seminalis (*ves. sem.*) into 3 parts and the long prostate are recognizable.

Structure of the Luminous Organs of *Cranchia* and *Liocranchia*

(Plate LX, Figures 1–11)

The luminous organs of *Cranchia* and *Liocranchia* (their arrangement was described on pp. 245–6) are of particular interest because they comprise ectodermal invaginations which remain connected with
343 the ectodermal epithelium throughout life. Among the Cranchiidae this is an isolated condition, present otherwise only in *Leachia.*

The luminous body (*phot.*) forms a pad which consists of several layers of ectodermal epithelium and is divided by a more or less deep slit that opens broadly to the outside. In *Cranchia* (Figures 1–3), the slit extends obliquely to the surface; in *Liocranchia* it forms either a flat, dish-shaped depression (Figure 8) or a more or less deep slit which opens broadly to the outside. Commensurate with the position of the slit, the organs of *Cranchia* form an acute angle with the body surface or are almost parallel to it. Sections of the organs show that they are about 3 times as long as wide. The organs of *Liocranchia* are lens- or dish-shaped; they are about twice as wide as long.

The luminous cells are usually slender, polyhedral, flattened, sometimes rounded at the edges. Sections show that there is a central cell at the bottom of the luminous body (Figure 10, *phot. centr.*) around which the other cells are arranged concentrically. Most of the luminous cells are elongate and radially arranged to the slit. The nuclei are generally small, rounded in the deeply situated cells, oval in the peripheral cells, with a few chromatin granules. The plasma is finely granulate in the deeper layers (Figure 9), while the outer cells around the widened opening of the slit are pale and vacuolated. As shown in the drawing (*Liocranchia*), there is no sharp boundary between the granulate cells and the cells with fluid content. The difference in the content of the cells is more distinct in *Liocranchia* than in *Cranchia.* These cells often have threadlike processes at the margin which pass into the flattend epithelium (Figure 11).

The deep slit resembles the lumen of a large gland. I thought at first that these ectodermal structures produce a luminous secretion as in the Sepiolini, the luminous organs of which were recently described by Meyer. This view seemed to be supported by the fact that the slit occasionally contains fine granulations which could be considered to have constituted a secretion. However, I abandoned this view. Similar granulations are present in other slits that have no connection with luminous organs

and the luminous cells, nor do they have the character of gland cells; they lack secretory vacuoles or granules which are present in the typical gland cells of Cephalopoda. It is also difficult to assume that a luminous secretion would be released between the eyeball and the eyelid which would have to exit through the pupil.

The luminous body is surrounded by a reflector (*refl.*) which usually consists of long, fiber-shaped cells. These cells pass gradually into spindle-shaped cells at the bottom of the organ and form con-
344 centric lamellae with an oval central nucleus. The long peripheral fibers of the reflector have only elongate nuclei which show all transitions to the oval form at the bottom of the organ. The outer surface of the organ between the reflector and the thin ectodermal epithelim is covered with a pad of loose connective tissue which consists of undulate lamellae (Figure 1, *spec.*). It resembles the subcutaneous tissue at points where a metallic sheen is present. This tissue causes the golden sheen around the organ and forms the mirrors on the luminous body of *Cranchia.*

The cross section of larger vessels is visible behind the reflector; these vessels are embedded in a thick part of the reflector in *Liocranchia* (Figure 8). Branches of the vessels pass through the reflector and enter the luminous body, where they form a fine capillary network (*cap.*) with flat, elongate nuclei which usually stain intensively. These nuclei usually differ distinctly from those of the luminous cells, especially in areas in which the nuclei are spherical. The capillaries usually pass between the luminous cells, but sometimes perforate them (Figure 10).

Neither in *Cranchia* nor *Liocranchia* I could find a pigmented layer around the reflector.

Joubin recently mentioned a polymorphism of the luminous organs of *Leachia.* I assumed a similar condition in *Cranchia* and *Liocranchia*, because of the relatively large number of luminous organs in *Cranchia.* This assumption is, however, not borne out by my findings. All organs show more or less the same structure and differ only in minor characters that do not represent polymorphism. There is only a trace of dimorphism in the two dorsal organs, which are smaller than the ventral organs. Their reflector is only weakly developed but the structure of the luminous body and the slit are exactly as in the other organs. As will be explained later, the polymorphism of the luminous organs of *Leachia* is not as marked as described by Joubin. I made sections of all 13 organs of the eye of *Cranchia*, taking due care of the sequence of the organs and the correct direction of sectioning. If this is neglected and the organs are sectioned obliquely, an apparent polymorphism may be present.

I assume that the organs do not emit different kinds of light. Since, however, the lid which extends over the organs contains chromatophores, it is possible that these give certain shades to the light which passes through them.

345

Juvenile stages of *Cranchia* and *Liocranchia*

Since I have often had occasion to observe live young Cranchiidae and also have had access to a relatively rich collection of preserved larvae of *Cranchia* and *Liocranchia*, I shall treat these juveniles jointly, beginning with their youngest stages.

At a length of 4–5 mm it is not yet determinable whether the larva belongs to *Cranchia* or *Liocranchia.* The larvae have only 6 arms of which the two larger ventral arms represent the tentacles (Plate LI, Figures 1–4). Strictly speaking, the arm apparatus thus consists of only the short 1st arms and the slightly longer 2nd arms. They bear only a few suckers, 1 or 2 pairs on the 1st arms and 3 to 4 pairs on the 2nd arms. That the next large arms to follow will develop into the tentacles is proved also by the fact that their tiny suckers are arranged in more than two rows, sometimes even in 4 distinct rows. The form

of these delicate, transparent larvae varies greatly: from bloated to pear-shaped to drawn-out and slender. The eyes are sessile and relatively large, so that the head appears wide. The funnel is of medium size, and the ventral fusion strips of the funnel and collaris are clearly visible. The small fins are spatulate and situated on the widened margin of the gladius.

Other, slightly larger larvae also have only the first two pairs of arms and the tentacles, but inasmuch as the first stellate tubercles are already present on the anterior ventral surface of the mantle, their genus can be determined as that of *Cranchia* (Figure 4).

In older larvae with a dorsal mantle length of 6–10 mm, all arms are already present. The stumps of the 3rd arms appear first, those of the 4th arms soon afterwards (Plate LI, Figure 7), so that the arm formula is 2, 1, 3, 4. However, the 3rd arms soon become longer than the 1st and also the 2nd arms (Figure 6), so that the arm formula becomes 2, 3, 1, 4 and 3, 2, 4, 1. The tentacles grow rapidly and show a distinct differentiation into stalk and club. Small suckers are present on the tentacle stalk from the base (Figures 6, 7).

The larvae of *Cranchia* of this stage can be distinguished with certainty from those of *Liocranchia* by the stellate tubercles. The differences between the two species of *Liocranchia* also appear early. Larvae of *L. reinhardtii* with a dorsal mantle length of 9.5 mm have already distinct dorsal spines which extend to the fins or to the point where the gladius widens. The larvae of *L. reinhardtii* also have 4 dis-
346 tinct chromatophores on the head, and the chromatophores on the mantle, some of which form distinct transverse rows, are more numerous than in *L. valdiviae*.

A typical larva of *Liocranchia reinhardtii* from the Indian Ocean (Station 217) is briefly described below.

The dorsal mantle length is 12 mm, the head is 2.5 mm wide. There are 25 dorsal spines. The tentacles are 6 mm long; the stalk bears 12 pairs of suckers from the base to the club. The arm formula is 2, 3, 4, 1; the 1st arms are very small and bear only 3 pairs of suckers.

The oldest larva of *Liocranchia reinhardtii* was caught in the Guinea Current (Station 54). The dorsal mantle length is 15 mm and its total length 20 mm. It bears 50 spines on the dorsum which extend to the cone of the gladius; there are also 15 spines on each of the lateral strips of fusions. The fins are rounded, as in *L. valdiviae*. The head (Plate LI, Figure 5) is widened by the relatively large eyes which look the more peculiar as preservation caused both lid folds to become baggy. The funnel extends to the base of the ventral arms and covers the small, sessile olfactory tubercles but not the 4 luminous organs visible below the lid fold.

The 3rd arms are slightly longer; formula: 3, 2, 4, 1.

The strong tentacle stalks bear 5 alternating pairs of suckers which reach almost to the base. There are 2 or 3 pairs of small, indistinct distal suckers near the club. The club shows the normal arrangement of quadriserial rows of suckers to the tip, which is curved dorsally in the form of a chamois horn; weak protective membranes are present, but a keel-shaped swimming membrane is absent.

Chromatophores are present in small numbers on the whole mantle; 4 large chromatophores are conspicuous on the dorsal side of the head. The tentacle stalks bear their whole length on the outer side two rows of chromatophores which unite near the club into a single row.

An older larva of *Cranchia scabra* (Plate XLIX, Figures 1–6) was collected south of Ceylon (Station 217). The pear-shaped mantle is 11 mm long and bears numerous tubercles, of which about 18 tubercles form a row along the gladius. The adjacent tubercles are arranged in parallel rows, the others irregularly. The tubercles on the fins are sparse and restricted to the base (Figure 5).

The fins are contiguous in the posterior part of the base and are only slightly longer than wide. Comparison with younger stages shows a gradual change in the form of the fins. The fins are at first

spatulate, wide and situated separately on the margins of the cone; later they become fused behind the
347 cone, forming a plate with a heart-shaped incision which finally projects slightly beyond the posterior end (p. 258). At the same time their length increases, so that in large specimens it comes to exceed the width.

The head is slightly retracted into the mantle; the funnel almost reaches the base of the tentacles (Figure 2).

The ventral arms (Figures 2, 3) are of special interest because they have just begun to develop and bear only a single sucker. The 3rd arms are slightly larger than the 1st and bear 3 to 4 pairs of suckers. The 2nd arms are the largest; they bear 4 pairs of suckers, the 1st arms only two pairs. The arm formula is thus 2, 3, 4, 1.

The length of the tentacles has considerably exceeded that of the arms; the tentacles bear biserial suckers from the base to the club which become gradually smaller distally. The suckers of the stalk pass gradually into the quadriserial arrangement of small suckers on the club (Figure 6). The protective and swimming membranes of the club are barely indicated.

This specimen resembles on the whole that illustrated by HOYLE (1904, Plate 10) from the material of the *Albatross* Expedition. HOYLE's specimen is a little older and has therefore a slightly greater number of suckers on the arms, but the arm formula is the same.

Leachia LESUEUR 1821

Leachia eschscholtzii RATHKE

(Plate LII, Figures 4–7)

Perothis eschscholtzii RATHKE, 1832, *Mém. Acad. Petersb.*, Vol. II, 1835, p. 149, Plates I, II.
Loligopsis cyclura FÉRUSSAC and D'ORBIGNY, 1835–1848, *Céph. acét.*, p. 322.
Loligopsis cyclura GRAY, 1849, *Catal. Ceph.*, p. 41.
Leachia ellipsoptera STEENSTRUP, 1861, *Overblik*, *Cranchiaeformes*, p. 80.
Perothis eschscholtzii ROCHEBRUNE, 1884, *Loligopsidae*, p. 19.
Leachia cyclura HOYLE, 1884, *On Loligopsis*, p. 326.
Leachia cyclura HOYLE, 1886, *Ceph. "Challenger"*, p. 46.

RATHKE, as already stressed in the General Part, was the first to provide a detailed anatomical description of a species of Cranchiidae. He named the species *Perothis eschscholtzii*. ESCHSCHOLTZ, who found it in the Indian Ocean (28° S, 310° W) named it *Perothis pellucida* in his diary. The complete transparency of the 3 specimens he caught enabled ESCHSCHOLTZ to make important observations of the live animal; these will be discussed below.

RATHKE's description, on the other hand, was largely ignored by later authors, although he gave a correct interpretation of the main character of the Cranchiidae, the fusion of muscular lamellae with the
348 mantle and their transformation into valves. I have attempted (pp. 5–6) to prove that RATHKE's "duplicature of the visceral sac" is homologous with the musculus depressor infundibuli, and his "valve", with the collaris. Although RATHKE's description of these typical conditions of Cranchiidae does not completely explain the actual conditions, later observers should have checked his data before criticizing him. At least the observation of ESCHSCHOLTZ, mentioned by RATHKE, that the two cavities direct the respiratory water to the gills and that a separate cavity leads to the funnel, should have been checked.

I examined a specimen of the forgotten *Leachia eschscholtzii* from the Zoological Collection in

Breslau. This specimen was collected in 1875* near Borneo, according to the label. d'Orbigny considered it at first as identical with *L. cyclura* and this was accepted by most later authors. However, the two species differ in the number of luminous organs on the eyes: there are 6 in *L. cyclura* and 8 in *L. eschscholtzii*, as correctly stated by Rathke. A common character of both species is the absence of tentacles the stump-shaped basal remnants of which are distinctly visible. I dissected this specimen as far as was possible without damaging it too severely, and can thus correct and complete Rathke's data on some points.

The specimen, a mature female, has a gladius of 73 mm length. In view of the fact that Joubin found numerous exhausted females of *L. cyclura* drifting on the surface during a cruise of the *Prince of Monaco* in August 1904, it may be concluded that *L. eschscholtzii*, too, is to be found on the surface only in exceptional cases, and only females during or after sexual maturation.

Mantle Complex

Opening of the mantle cavity shows the delicate visceral sac, which tapers posteriorly into a narrow point (Plate LII, Figure 4). The stomach, caecum, ovary (*ov.*) and the very long gastro-genital ligament (*lig. g. g.*) are visible through the thin abdominal wall. Above the organs extends the aorta posterior. The renal sac forms two raised, chimney-like papillae (*ur.*), which were not noticed by Rathke. Anterior to the papillae there are the rectum and the anus with its lanceolate appendages. The gills are of medium size; they are surrounded anteriorly by the spiracula, i.e. the opening of the dorsal mantle sacs. The vena cava (*v. c.*) is visible anteriorly and is sinuate, while the arteria posterior (*a. p.*) takes a straight course on top of the posterior part of the visceral sac. The mature glands of the female gonoducts cover a large part of these organs. The right oviduct gland (*gl. od. d.*) is broadly open, while the two arms of the left gland (*gl. od. s.*) are situated close together. Behind the oviduct glands lie the relatively large nidamental glands (*nid. d.*); they are covered with numerous chromatophores.

349 Intestinal Tract

The intestinal tract shows very characterisitc conditions, which were correctly interpreted by Rathke. The long, thin esophagus (Plate LII, Figure 5, *oes.*) surrounds the posterior dorsal side of the liver and opens ventrally far from the liver into a sinus at the junction of stomach and caecum. The large opening which leads into the caecum (*st. coec.*) is visible shining through the sinus. The caecum is sac-shaped; it is covered anteriorly by the pancreas and extends to the ovary. The caecum is very considerably larger than the stomach. The stomach begins widened as a tube behind the entrance of the esophagus, then continues as a narrow duct with folds (*st.'*), swelling to pear shape only a short distance before the ovary (*st.*). The weakly developed folds (Figure 7, *rad.*) on the dorsal side of the posterior end of the caecum lead to two swellings which extend in a curve to the beginning of the rectum (Figure 6, *sulc.*). From the beginning of these swellings extends a short longitudinal fold (not shown in the figure) which continues to the ventral surface. This fold is crossed by a sickle-shaped transverse fold (*vel.*) between the widened tubular beginning of the stomach and the entrance to the

* Editors' note: 1875 is an incorrect date, undoubtedly a typographical error. The specimen was probably captured during the *Rurik* Expedition in 1815. [C.F.E.R.].

caecum. The mid-intestine (*int.*) begins at the common gastric sinus before the opening of the esophagus and extends in a half-spiral around the long hepatic duct, then passes on the ventral median surface of the liver and finally into the elongate, slightly narrowed rectum (*rect.*), which has a pear-shaped widening prior to the anus, and lanceolate appendages (*app. an.*) lateral to the anal lips.

The spindle-shaped liver (*hep.*) has a shining capsule. It is 10 mm long and stands upright, nearly along the longitudinal axis of the body. Close to the rectum on both sides of the posterior third of the liver the openings of the sac-shaped, thin-walled hepatic ducts (Figure 5, *d. hep.*) are situated. These ducts unite at about the level of the dorsal posterior apex of the liver into a single duct (*d. hep. c.*) which is very long in the specimen examined and opens into the caecum slightly above the beginning of the rectum; the single duct bears two large clusters of pancreatic glands (*pancr.*). The only other genus that has such a wide distance between pancreas and liver is *Euzygaena*. The pancreas seems to consist of a single glandular mass, but does in fact consist of two parts (Figure 7, *pancr.*) which are nearly contiguous dorsally but widely separated ventrally, between esophagus and mid-intestine. The glands consist of thin-walled, repeatedly sinuate follicles which are fused and open into the terminal part of the hepatic duct with numerous large openings (Figure 6, *d. panc.*). The large gastric ganglion (*g. visc.*) is situated between the pancreas and the opening of the esophagus.

The major features of the intestinal tract were correctly described by Rathke. In particular, he was right in emphasizing the large "pyloric vesicle", which he compared to the spiral stomach or caecum of
350 the Octopoda. Rathke also described the confluence of the two hepatic ducts into a common duct and the "pyloric appendages" (pancreas) at the opening of this duct into the caecum. However, Rathke overlooked the ink sac, which was observed by Eschscholtz in the live animal.

The data of Grant on the intestinal tract of *Loligopsis* (*Leachia*) *guttata* are so absurd that a detailed discussion is hardly worthwile. It is hard to explain why he states that the liver consists of 4 separated packets of glands, unless Grant considered the nidamental glands as the liver and the liver as the ink sac.

Vascular System

The vena cava has a sinuous course in the preserved specimen; it ascends on the right side above the liver and opens in the venous sacs. These are omitted in Figure 5, so as to avoid complication of the figure. They show on the whole the same arrangement as in *Cranchia*, and we note only briefly that the vena cava enters a small sac which borders on a larger triangular sac. From the corners of this sac extend the branchial arteries in an anteriorly convex curve. There are also two sacs of the hepatic veins, an anterior and a posterior one, and a large median sac which is situated on the hepatic ducts and receives the gastric vein. Other venous sacs are formed by the branchial arteries before they open into the branchial hearts.

The branchial hearts are rounded and completely covered by the nidamental glands. The moderately large gills are loosely arranged; from them extend the thin-walled branchial veins which are slightly dilated where they open into the heart (Figure 5); the latter is cylindrical, tapering at both ends and not widened at the entrance of the branchial veins. The heart is situated on the ventral side of the liver, slightly oblique to the longitudinal axis. The cephalic aorta extends from it dorsally. It has a spindle-shaped base and branches into the hepatic artery (*a. hep.*) and the dorsal artery (*a. dors.*). The gastric artery (*a. g. g.*) branches from the beginning of the cephalic artery close to the apex of the heart. This artery extends posteriorly on the single hepatic duct, where it is partly covered by the pancreas, and extends near the gastric ganglion in a straight course toward the caecum and stomach.

From the ventral end of the heart extends the posterior artery (*a. post.*), at the base of which begins the thin anterior artery. The posterior artery branches posteriorly into the pallial artery and then bifurcates to form the two arteries of the fins. This condition was more distinct in the closely related *Euzygaena*, in which the pallial artery also originates far posteriorly, close to the bifurcation into the arteries of the fins.

Rathke incorrectly considered the confluence of the venous sacs as the heart, and because of this mistake he considers all arteries as veins and vice versa and also expresses his surprise that the branchial
351 heart ("lateral heart" in his terminology) is not situated on the vessel which carries blood to the gills but on that which carries blood from them. Grant gives a more correct interpretation, although his description of the venous sacs is incomplete.

Genital Organs

The female genital organs consist of the ovary, the oviducts with the oviduct glands, and the nidamental glands.

The ovary (*ov.*) is visible shining through the visceral sac. It is large, oval, 9 mm long, situated dorsally behind the two parts of the stomach which partly cover its anterior half. It continues in a long cord of connective tissue (*lig. g. g.*) which can be followed to its attachment on the cone of the gladius.

The winding oviducts are situated at some distance from the ovary. I observed that they contained eggs measuring 1.2 mm in diameter. The oviducts pass dorsal to the base of the gills and open in two large terminal parts. These structures are the oviduct glands, which are very large in this mature female (Figure 4, *gl. od. d., gl. od. s.*). The right oviduct gland has two broadly diverging arms; it covers the base of the right gill and also the renal sacs to the anus and the vena cava. The arms of the left oviduct gland are situated close together and also extend over the gills and adjacent parts. The inner surface of the oviduct glands bears distinct glandular lamellae; the outer side is smooth and covered with numerous dotlike chromatophores.

Behind the oviduct glands are the nidamental glands (*nid.*), which are large, too. Noteworthy is here, again, that the two arms of the horseshoe-shaped glands diverge broadly, and that, like the oviduct glands, they bear regular glandular lamellae. Comparison with a specimen of *Euzygaena* shows that this condition apparently develops early. The horseshoe-shaped nidamental glands are held together by a delicate lamella with numerous chromatophores; this lamella soon bursts near the opening of the gland, causing the arms of the gland to curve like a lyre and to expose the inner surface with its glandular lamellae. The slit between the two arms is perpendicular to the surface of the body.

Since mature females of Oegopsida other than *Leachia* are not known, it is possible that the condition of the oviduct and nidamental glands described applies to the whole order. In most Oegopsida
352 the swelling of the glands and the tearing of the delicate membrane which envelops them take apparently place only shortly before oviposition, while in the Cranchiidae this process takes place much earlier.

These conditions have led to a number of erroneous interpretations. As already mentioned, Grant's statement of a liver which consists of 4 parts is apparently due to a confusion with the nidamental glands. Rathke, though illustrating the 4 glands correctly and interpreting them as "organs of secretion", did not recognize their relation to the female genitalia. He observed the connection between the winding oviducts and the oviduct glands and interpreted the former, too, as organs of secretion. Lönnberg (1896, p. 612) was the first to recognize the nidamental glands; he, however, erred in considering the oviduct glands to be accessory nidamental glands.

Luminous Organs

My study of the luminous organs of *L. eschscholtzii* was suggested by the detailed description of the luminous organs of *L. cyclura* by Joubin (1905). His observations are of interest not only because they comprise the only exact data available on the luminous organs of the Cranchiidae, but also because they provide the most reliable character for the distinction of the two species of *Leachia*. Joubin also records a surprising polymorphism in *L. cyclura*: he states that the 6 organs belong to 5 different structural types! Before discussing these data in greater detail it should be noted that 5 of the 6 organs on the eyball form an outer row on the ventral margin, while the 6th is situated singly, close to the lens. For *L. eschscholtzii* Rathke stated correctly 8 organs, 6 in an outer row and the other two near the margin of the lens. He failed, however, to recognize them as luminous organs but assumed these pearl-like structures to be ganglia.

I made sections of 3 of the 8 organs of *L. eschscholtzii*—two inner and one outer organ. The organs do not show the polymorphism stressed by Joubin but are identical in all essential characters. A median organ of the outer row (Plate LX, Figure 12) will be described first. The preservation of the material was better than I assumed at first. There is a large oval luminous body (*phot.*) situated obliquely to the outer surface and contiguous with the inner side of the eye cartilage (*cart.*). As in *Cranchia* and *Liocranchia*, the luminous body represents an ectodermal invagination which retains its constant connection with the outer epithelium of the body. A deep slit is apparently absent. However, the outer opening of the organ has a groove which corresponds to the slit of the organs of *Cranchia*. This groove is bordered by elongate cells which spread in a fan and contain distinct nuclei. These cells flatten rapidly where they pass into the ectodermal epithelium (*ek.*).

353 The luminous body consists of two layers which pass gradually into each other. The deeper inner layer consists of polyhedral cells with a homogeneous, finely granulate plasma and small spherical nuclei. These cells stain more intensively than the peripheral layers, in which the cells are also polyhedral but more vacuolized and therefore stain less intensively. The polyhedral cells pass gradually into the marginal cells, which are arranged in a fan. Joubin considers these lighter cell layers to be a lens, and the deeper layers to be the true luminous cells. According to his description and drawings, the two categories of cells are sharply differentiated from each other. *Leachia* resembles *Cranchia* and *Liocranchia* in this respect because there is no sharp distinction between the peripheral and central cell layers; the only difference, a minor one, is that the nuclei of the deeper cell layers are slightly smaller than those of the peripheral layers.

The organ is surrounded by a reflector (*refl.*) which is thick at the bottom but flattens gradually toward the periphery. The outer layer of the reflector is slightly thicker than that situated on or close to the eye cartilage. The cells of the outer layer have nuclei which stain intensively; they are spindle-shaped and form loose concentric lamellae. These cells become longer toward the periphery and finally form fibers.

The organs have a rich vascular supply. Numerous fine capillaries (*cap.*) pass through the luminous body at the margin of the organ, often in a straight course. I observed a larger vessel at the margin of the light peripheral cells, but was unable to determine whether this is the vessel where the blood supply originates; I should add, however, that cross sections of larger vessels (*v.*) are visible also behind the reflector.

I failed to find the peripheral cartilaginous ring which, according to Joubin, supports the organ. I assume that such a ring does not exist and the structure referred to is the iridescent layer of connective tissue mentioned already in connection with the organs of *Cranchia* and *Liocranchia*.

Although the conditions observed in *L. eschscholtzii* are not necessarily identical with those in

L. cyclura, the organs of *L. cyclura* are not as polymorphic as Joubin believes. It must be emphasized that the orientation of sectioning of these oval organs is decisive, because oblique sections may easily lead to wrong conclusions. It is also advisable to remove the eyelid fold before sectioning, otherwise this duplicature may appear to be firmly fused with the anterior surface of the organ, as was, indeed, asserted by Joubin for some organs. Joubin's descriptions and figures suggest that the reflector of the organs of *L. cyclura* are distinguished by a constriction which in one organ is so marked that a part of the luminous body becomes separated. This, in my opinion, is the only distinct difference between the organs of *L. cyclura* and those of *L. eschscholtzii*. The other assumed differences are caused, at least in part, by an incorrect orientation of the section and by the fact that in one organ the lid fold with its
354 chromatophores was removed and in the other, not. In the latter case, Joubin considered the lid fold as a special layer which covers the organ and named it cornea. If, furthermore, even organs which have a pupil are being considered as a special type, then one should note that this condition is present in all organs of *Leachia* and *Liocranchia*; for sections obtained by cutting obliquely through the groove at the peripheral inner margin produce the pictures shown in Joubin's Figure 7. That this condition is not restricted to *Leachia* is shown by comparison with *Liocranchia*, in which some of the marginal cells of the luminous body protrude above the central layers (Plate LX, Figure 8).

I conclude, therefore, that the luminous organs of *Leachia* are not as polymorphic as those of some Enoploteuthidae or Chiroteuthidae.

Euzygaena Chun

Euzygaena pacifica Issel
(Plate LII, Figures 1–3)

?Loligopsis zygaena Vérany, 1851, *Céph. Médit.*, p. 125, Plate XL, Figure c.
?Zygaenopsis zygaena Rochebrune, 1884, *Loligopsidae*, p. 14.
?Pyrgopsis rhynchophorus Rochebrune, 1884, *ibid.*, p. 17, Plate II, Figures 1–6.
?Loligopsis schneehagenii Pfeffer, 1884, *Ceph. Hamb. Mus.*, p. 23, Plate III, Figure 31.
?Loligopsis zygaena Hoyle, 1886, *Ceph. "Challenger"*, p. 46.
?Zygaenopsis zygaena Pfeffer, 1900, *Syn. Oeg. Ceph.*, p. 193.
Zygaenopsis pacifica Issel, 1908, *Cef. "Liguria"*, p. 223, Plate X, Figures 33–44.
?Zygocranchia zygaena Hoyle, 1909, *Catal. rec. Ceph.*, 2nd Suppl., p. 276.

In his *Céphalopodes de la Méditerranée*, Vérany illustrated a small cephalopod with stalked eyes. He described this specimen as *Loligopsis zygaena* on the suggestion of Krohn, from whom he had received the specimen. The drawing shows what seems to be a delicate Cranchiid, most likely belonging to the genus *Taonidium*. The description, however, is so incomplete that later workers found it difficult to determine its systematic position. Rochebrune (1884, p. 14) created for it the genus *Zygaenopsis* and named it *Z. zygaena*. Hoyle (1884, *On Loligopsis*, p. 331) disagreed, mainly because the name *Zygaenopsis* is preoccupied by Felder (1874) for a genus of Lepidoptera. Pfeffer (1900), however, retained the name *Zygaenopsis* for a small form which he had described as *Loligopsis schneehagenii*. Pfeffer gave the following diagnosis:

> "Mantle on each side with a single longitudinal ridge, dorsal ridge absent; fins attached at
> 355 sides of mantle.—Mantle membranous; fins rather small, rhomboidal; eyes moderately large, stalked in the form of a club; anterior part of head long, narrow (olfactory papilla?); tentacles present."

In the description PFEFFER also noted that the ridges on the mantle bear stellate tubercles and that the 3rd arms are longer than the others. PFEFFER considers this specimen to be identical with *Loligopsis zygaena* VÉRANY, although VÉRANY's description and drawing show the arms to be about equal length, the 3rd arms not being larger than the others.

PFEFFER, furthermore, considers this species to be identical also with *Pyrgopsis rhynchophorus* ROCHEBRUNE, 1884. This consideration appears to be based on ROCHEBRUNE's statement that there is a ridge with 4-radiate tubercles at the sides of the mantle. Otherwise, the drawings and descriptions here, too, are so incomplete that it is difficult to determine the systematic relation to the form described by PFEFFER. If now PFEFFER considers *Taonius richardi* JOUBIN (1895, p. 46, Plate III, Figures 5, 6), too, to be identical with *Z. zygaena*, he is certainly referring to a young *Taonidium* in which the suckers of the median row of the club have already begun their transformation into hooks.

I have two specimens of Cranchiidae that agree with PFEFFER's definition of *Zygaenopsis* in all important points. One of them was caught by the German South Polar Expedition in the Atlantic Ocean; the other was obtained by DOFLEIN in Sagami Bay, Japan. The Atlantic specimen, caught close to the surface at night, is severely damaged, in particular by loss of the eyes. The Japanese form, however, is in perfect condition and is illustrated here with DOFLEIN's permission. According to my earlier diagnosis (1906, p. 84), the characters of the genus *Euzygaena* (*Zygaenopsis*) are as follows:

> Body slender, membranous. Ventral surface of mantle having a ridge covered with tubercles on each side. Fins forming together an almost circular or transversely oval disk, ending level with the apex of the body. Posterior end of gladius forming a narrow cone. Pancreas situated far from the liver, directly on the caecum at the end of the hepatic duct.
>
> Eyes small, oval, with long stalks, produced into a ventral process; stalks plump, ovoid; head pillar long. Suckers on the tentacle club larger in the median rows than in the marginal rows. Third arms large. Right ventral arm hectocotylized, longer and thicker than the left, with a strong keel and dense biserial suckers.

I propose the generic name *Euzygaena*, because *Zygaenopsis* is preoccupied. While this monograph was in press, however, I obtained the Second Supplement to the *Catalogue of Recent Cephalopoda* by HOYLE (1909), in which the same genus is named *Zygocranchia*. To avoid confusion, I have nevertheless retained the name *Euzygaena* which I have used in the text and on the plate.

356 A detailed description of the two specimens will be given elsewhere. Here be it only noted that the specimen from Sagami Bay has a dorsal mantle length of 47 mm.

Of all the forms described so far, this specimen seems nearest related to *Zygaenopsis pacifica* ISSEL, although there are some differences; these however seem to be secondary. The other species so far suggested are so insufficiently characterized that their relation to *Euzygaena pacifica* cannot be determined without examination of the types.

Desmoteuthis VERRILL, 1881

Leachia hyperborea STEENSTRUP, 1856, *Vid. Selks. Skrift.*, 5, R. IV, p. 200.
Taonius hyperboreus STEENSTRUP, 1861, *Overblik Cranchiaeformes*, p. 83.
Desmoteuthis tenera VERRILL, 1881, *N. Am. Ceph.*, p. 412, Plate LV, Figures 2–2d; Plate LVI, Figure 3.
Megalocranchia maxima PFEFFER, 1884, *Ceph. Hamb. Mus.*, p. 24, Plate III, Figures 32, 32a.
Taonius hyperboreus HOYLE, 1886, *Ceph. "Challenger"*, p. 191, Plate XXXII, Figure 12; Plate XXXIII, Figures 1–11.
Taonius abyssicola GOODRICH, 1896, *Ceph. Calcutta Mus.*, p. 17, Plate V, Figures 72–80.
Desmoteuthis hyperborea, abyssicola, maxima PFEFFER, 1900, *Syn. Oeg. Ceph.*, p. 192.

Desmoteuthis Chun, 1906, *Syst. d. Cranchien*, p. 85.
Desmoteuthis abyssicola, hyperboreus, maxima **Hoyle, 1909,** ***Catal. rec. Ceph.*****, 2nd Suppl., p. 277.**
Desmoteuthis hyperborea Massy, 1909, *Ceph. Ireland*, p. 33.
Helicocranchia pfefferi Massy, 1909, *ibid.*, p. 34, Plate III.

The genus *Desmoteuthis* was established in 1881 by Verrill (p. 300). The species on which this genus was based, *D. hyperborea*, is apparently identical with *Taonius pavo* Les. (Hoyle, 1884, *On Loligopsis*, p. 316). In a later part of his work (p. 412, Plate LV, Figure 2), Verrill described a second species, *Desmoteuthis tenera*, which is probably identical with *Taonius hyperboreus* Steenstr. Hoyle therefore thinks that the genus *Desmoteuthis* should be united with *Taonius*. Although there is certainly a close relationship between these two genera, I agree with Pfeffer (1900, p. 189), who believes that the genus *Desmoteuthis* should be retained and should include 3 species: *D. hyperborea*, *D. abyssicola* Goodr. and *D. maxima* (*Megalocranchia maxima* Pfeffer).

The differences between the genera *Desmoteuthis* and *Taonius* consist mainly in that in *Taonius* the end of the gladius projects like an arrow beyond the fins while in *Desmoteuthis* it ends level with the dorsal base of the fins. Furthermore, in all specimens of *Taonius* examined so far, the tentacles are missing and the gelatinous mantle is vividly pigmented, while in *Desmoteuthis* the tentacles are present and the transparent, membranous body bears sparse chromatophores (p. 239).

I include a 4th species in the genus *Desmoteuthis*; it is closely related to *D. maxima* Pfeffer and differs from it mainly in the form of the denticles on the suckers. According to Pfeffer, the suckers of the
357 club of *D. maxima* bear 10 narrow, pointed hooks, while those of *D. pellucida* show a variable number of blunt indentations.

As stated above (p. 237, n.), I consider *Helicocranchia pfefferi*, recently described by Massy, to be a species of *Desmoteuthis*, too. This species differs from the other species of *Desmoteuthis* mainly in the form of the fins, which are situated seperately with a narrowed base on the posterior end of the body and project beyond it. The form of the fins of this species resembles that of *Corynomma*; however, all other characters agree with those of *Desmoteuthis*. I believe, therefore, that further material will have to be obtained before a new genus can be established.

Desmoteuthis pellucida Chun

(Plate LIII, Figure 1; Plate LIV, Figures 1–17)

Locality: Station 90: Benguela Current, 33°20′ S, 15°58′ E. Vertical net to 1,000 m—One female.

In the southern Atlantic we caught a species of the genus *Desmoteuthis* that was the most transparent of live specimens I have examined. The animal was exhausted; the posterior end of the body was invaginated into the mantle, so that only part of the fins projected. I kept it alive for some time in cooled seawater and made several drawings which are shown in natural size on Plate LIII. After preservation, the body swelled, the lids came to cover the eyes completely and the tentacles shortened by one-third. The live animal was 130 mm long and the tentacles were 40 mm long. The figure shows the normal habitus. The spindle-shaped mantle projects far toward the short head with its markedly protruding eyes; the transparent, chimney-shaped funnel almost reaches the base of the arms. The scattered chromatophores on the mantle became strongly contracted during preservation; the figure shows them expanded as in the live animal. In addition to the transparent inner organs, the magnificent metallic sheen of the envelope of the liver was striking. The liver is situated almost perpendicular to the longitudinal axis of

the body. The whole mantle was covered with a transparent layer of slime which shrank during preservation, forming a whitish cover; the latter swelled up again whenever the specimen was placed in dilute alcohol or in distilled water.

Mantle

The mantle has a dorsal length of 77 mm, which is also the length of the gladius. The mantle is fleshy and thin-walled and ends posteriorly in a blunt tip. In the live animal, the inner organs and the insertion
358 of the collaris and the funnel depressors (described in the introduction) were visible through the mantle. In the attitude normally assumed, the mantle resembles the bowl of a longish goblet with narrowed brim. Contraction of the circular muscles results in a more cylindrical form; the contraction during preservation causes inflation of the body. The dorsal and ventral corners of the mantle margin are barely visible in the live animal; the dorsal point of fusion of the mantle is slightly retracted in the preserved specimen and the free margins project beyond it.

The secretion of a gelatinous substance led me to undertake a more detailed study of the structure of the mantle, particularly of the ectoderm. The results are as follows:

A longitudinal section of the mantle (Plate LIV, Figure 10) shows that it consists of 4 layers of different thickness. Beneath the outer ephithelium (*ek.*), there is a layer of subcutaneous connective tissue (*bg.*); this consists of a thicker outer layer (*bg.*^{1}) which has nuclei of irregular form, and a thinner inner layer (*bg.*^{2}) which has no embedded cells. Then follows the 3rd, thickest layer, which is that of the strongly developed mantle musculature. Finally, there is a thin 4th layer (*lam. int.*) which faces the respiratory cavity.

I shall describe each of these layers separately, starting with the outer epithelial layer. I had assumed that the cover of slime is produced by special gland cells in the ectoderm; this proved to be incorrect: rather does the entire ectoderm take part in the secretion of slime. Examination of the ectoderm from the surface shows that there are no sharp boundaries between the cells; only the regularly distributed nuclei indicate the territories of the cells. The nuclei (Plate LIV, Figure 11) vary markedly in form: some are indented, others are lobed or grossly ramified. Their content is homogeneous, lacking larger granules of chromatin. The section through the skin shows the borders of the cells more distinctly because there are light gaps between the cells.

The finely granulate plasma forms numerous short processes toward the cutis (Figure 10, *ek.*). In cells whose plasma extends to the cutis, the processes are indicated only by striation of the cell content. The cells of the ectoderm are generally cube-shaped and do not resemble gland cells; nevertheless they do apparently secrete the layer of slime that covers the entire outer epithelium.

The second layer consists of subcutaneous connective tissue. Its thick outer layer contains nuclei of irregular form which are often indented or elongate. This layer is regularly stratified parallel to the surface and contains capillaries. Between this layer and the musculature is a light stripe (*bg.*^{2}) which has neither fibers nor nuclei but intermittently shows a fine honeycomb structure.

The thickest layer of the mantle is formed by muscles of a structure typical for all Oegopsida. These are the radial muscles (*mu. rad.*) which at regular intervals cross a layer of circular muscles (*mu. circ.*).
359 The circular muscle fibers are densely arranged and appear rounded or oval in cross section. These fibers have a contractile sheath and a finely granulate core with very long nuclei (Figure 9, *mu. circ.*). The radial fibers (*mu. rad.*) are united in the middle of the mantle into a contractile, irregularly sinuate lamella (Figure 10, *lam. rad.*) with large nuclei (*nu. rad.*) which are of irregular form, flattened and partly

hatchet-shaped. The thicker muscular cords which radiate from the center are often once or twice bifurcated and extend straight between the circular fibers to the cutis. Different views are obtained depending on whether the section is parallel (Figure 9) or perpendicular (Figure 10) to the circular fibers.

The layer (*lam. int.*) facing the respiratory cavity consists of a thin cutis and a thin layer of epithelium.

The **fins** of the live animal were retracted into the posterior end of the body. When the fins were returned to their normal position I obtained the following picture. Each fin is more or less half-oval, 15 mm long and 8 mm wide. The dorsal bases of the fins diverge anteriorly and surround the cone, which is 8 mm wide. The dorsal bases of the fins are fused in their posterior half into a rounded plate which projects about 4 mm beyond the gladius. They resemble the fins of adult *Cranchia* and *Liocranchia*, and especially those of *Desmoteuthis maxima* as illustrated by PFEFFER.

The **gladius** is visible through the mantle. It has a narrow anterior part; the posterior part is about 22 mm long and widens gradually to 5 mm anterior to the base of the fins.

Head and Funnel

The head is short and plump, 6 mm long from the dorsal point of fusion of the mantle to the base of the arms and is 18 mm wide, which is due mainly to the markedly protruding eyes.

The eyes (Plate LIV, Figures 7, 8) are oval; their width measures 9 mm, their transverse axis, 7 mm. They protrude almost in their entirety, while their large optic ganglia are situated inside the head. The iris of the live animal had a metallic sheen and a wide open pupil. The lid fold of the preserved specimen covered the eye completely, leaving only a small slit open (Figure 3). Each eye bears two large luminous organs on the ventral side, which will be described below. The posterior organ (Figure 8, *luc. post.*) is crescent-shaped, 5 mm wide and 4 mm long. A smaller, sickle-shaped organ (*luc. ant.*) is invaginated in the concave anterior margin of the posterior organ. The small olfactory tubercle (Figure 3, *tub. olf.*) is revealed on the posterior margin of the eye; it is pear-shaped in profile and situated on a very short, plump stalk (Figure 6).

360 The **funnel** of the live animal is straight and projects to the base of the arms like a chimney. A funnel valve is absent; the funnel organ has a shovel-shaped single dorsal part (Text Figure 32b; p. 245). The funnel organ forms posteriorly two rounded lobes which surround the vena cava; it has a spatulate tubercle on these lobes and a lanceolate tubercle in its middle. The paired ventral parts of the funnel organ are crescent-shaped or nearly oval and much smaller than the single part.

Arm Apparatus

The arms (Plate LIV, Figure 1) are moderately large and differ only little in length. The 1st and 4th arms are about equal—13 mm long; the 2nd arms are 16 mm, and the 3rd arms 19 mm long. The arm formula is thus, 3, 2, 4, 1.

The arms bear the following numbers of pairs of suckers (counted on the left arms): The 1st arm has 12 larger pairs of suckers, followed by 3 smaller pairs at the tip. The 4th arms has 12 pairs of suckers which decrease gradually in size. Some pairs of suckers on the 2nd and 3rd arms are larger than the others. On the 3rd arms there are at first 9 pairs of suckers of about the same size; they are followed by 3 larger and more widely spaced pairs and finally by 4 pairs which decrease rapidly in size, totalling

16 pairs on the 3rd arm. The 2nd arms bear 14 pairs of suckers, of which the 11th, 12th and 13th pair are slightly larger and situated at greater intervals than the preceding ones. All suckers show indistinct indentations, about 9 on the largest suckers (Figure 5). The identations gradually pass into a ridge on the proximal side of the suckers. The indentations of a dried sucker appear whitish. A whitish coloration is present also in the interior of the distal half of the sucker. The absence of denticles and their replacement by indentations is characteristic of *D. pellucida.* All arms have broad protective membranes and their strong muscular supports alternate with the suckers. These membranes unite between the two 1st arms without forming a "sail"; between the 1st and 2nd arms they are almost contiguous at the base. The swimming membranes are very weakly developed, except for the distal part of the 4th arms, where they are slightly more distinct.

The **tentacles** of the preserved specimen have a length of about 25 mm, 7 mm of which are taken up by the club. The tentacle stalk is rounded proximally but gradually flattens on the inner side before it passes into the slightly widened club. A median groove is scarcely indicated. The stalk bears 14 groups of 4 suckers in a zigzag pattern. Distally the groups gradually increase in size and pass into the characteristic rows of 4 suckers on the club without forming a distinct carpal part. There are 19 rows of 4 suckers on the club, of which the median ones are larger than the preceding or succeeding ones.

361 The suckers on the club (Figure 4), like those on the arms, lack distinct denticles. They, too, have, however, indentations, which are larger in the distal half than in the proximal half. There are about 20 indentations on the larger suckers, fewer on the smaller suckers. The club is curved dorsally like a chamois horn. It has a sharp keel which is also displaced to the dorsal side (Figure 2). The protective membranes of the club are well developed, particularly the ventral protective membrane, the muscular supports of which are almost contiguous.

The attachment of arms and tentacles shows the typical condition of the Cranchiidae.

Coloration

As already emphasized, no other live cephalopod that I observed was even nearly as transparent as *D. pellucida.* Even the peristaltic movements of the stomach were distinctly visible. Thus the chromatophores of *D. pellucida* are correspondingly weakly developed. A median row of chromatophores is situated on the mantle along the gladius. Scattered yellowish chromatophores are also present on the mantle. They form an indistinct arrangement in 6 transverse rows on the anterior half of the mantle; from the 7th to the 14th row the transverse arrangement is gradually altogether obliterated. The fins and funnel are not colored. There is a single row of chromatophores on the outer side of the arms and tentacles, including the club; the protective membranes of the club also bear a few tiny chromatophores. The head part shows small scattered chromatophores and two particularly large chromatophores on the dorsal side of the eyes at the level of the optic ganglia.

Inner Organization

INTESTINAL TRACT

The esophagus (*oes.*) is surrounded by the cephalic vein and accompanied by the cephalic aorta; it extends obliquely along the diaphragm ventrally and opens far from the liver into a part of the stomach

(Plate LIV, Figure 12, *st.str.*) which widens in the form of a funnel and opens into the large, thin-walled stomach (*st.*). The funnel-shaped part contains very strong longitudinal folds (Figure 17), among them two larger swellings (*str.*[1]). In the live animal, this part made peristaltic movements. The folds disappear toward the stomach, which has thin walls and is attached to the mantle at the level of the widening part of the gladius by a dorsal ligament (*lig.g.g.*). Opposite the opening of the esophagus there is the relatively small caecum (*st.coec.*), which contains numerous large folds, especially in its anterior part (Figure 17). The caecum passes broadly into the mid-intestine (*int.*), which extends on the left of the esophagus to the ventral side of the liver and becomes narrower only near the ventral end of the liver (Figures 12, 14, 15) where it passes into the rectum (*rect.*). The mid-intestine contains weak
362 longitudinal folds its whole length and, at its beginning, two longitudinal swellings which extend from the folds of the caecum and lie on top of the hepato-pancreatic duct, enclosing a deep groove (Figure 17, *sulc.*). These swellings are visible shining through opposite the opening of the hepato-pancreatic duct (Figure 16). The rectum curves around the end of the liver and opens between the two broad anal lips. The anal appendages (*app.an.*) are relatively large and have broad, slightly asymmetrical lateral lobes.

The liver (*hep.*) has an envelope with a metallic sheen. It is spindle-shaped, tapering uniformly at both ends and situated almost perpendicular to the longitudinal axis of the body; its ventral end projects for some distance into the respiratory cavity. The efferent ducts of the liver originate on the dorsal third of the organ (Figure 15, *o.pancr.*); they are unusually long and covered their whole length by pancreatic glands (Figure 12, *pancr.*) which decrease gradually in size. This condition is more striking in *Desmoteuthis*, and probably also in *Taonius*, than in any other cranchiid.

As regard the pancreatic follicles, the 2 anterior ones (Figure 12, *pancr.ant.*), situated directly at the exit of the ducts, are the largest; these two follicles consist of indistinctly differentiated lobes. The other follicles are at first arranged in 3 rows, then indistinctly in 2 rows and extend to the caecum. The gastric vein is visible shining through on the ventral side between the 2 rows of gland complexes (Figures 14, 15, *v.g.g.*).

The cross section through the mid-intestine and the hepato-pancreatic duct close before the caecum (Figure 13) shows dorsally the mid-intestine (*int.*) with its weak longitudinal folds and the esophagus (*oes.*) on the right side. Ventrally passes the hepato-pancreatic duct (*d.hep.pancr.*), the walls of which are markedly thickened on both sides and contain the pancreatic appendages. The gastric vein (*v.g.g.*) extends on the ventral side of the duct.

VASCULAR SYSTEM

The vena cava (Plate LIV, Figure 12, *v.c.*) appears directly behind the middle part of the funnel organ on the ventral side, follows thereafter a slightly sinuous course to the liver and circumscribes the latter on the right side in a wide curve, to finally open into venous sacs, which in *Desmoteuthis* are particularly well differentiated. The vena cava opens first into a sac (*sacc.v.post.*) which also receives the cephalic vein (*v.ceph.*), which was unusually inflated in this specimen; the cephalic vein is curved like a horseshoe at the point where it leaves the esophagus (Figures 12, 15). The dorsal vein (*v.dors.*) joins this curve, while the pancreatic vein (*v.pancr.*) enters it at the point where it widens into the spongy venous sac (Figure 15, *sacc.v.post.*). Close to the right of this venous sac, near the mid-intestine, there is a slightly smaller sac (Figure 15, *sacc.g.g.*) which receives the gastric vein (*v.g.g.*) the branches of which are especially distinct on the caecum (Figure 16). The confluence of this sac with that of the vena
363 cava and the dorsal vein is covered by a large sac which receives the hepatic vein (*sac.v.hep.ant.*) from

the anterior direction and also passes close to the right of the mid-intestine. This sac branches into the two large branchial arteries (*a. branch.*). Two cardiac veins (Figure 14, *v. cord.*) open symmetrically into the base of the branchial arteries at the point where the venous sacs show the spongy structure at the base. The penetration of the cardiac veins into the heart, with the numerous branches which it forms thereon, was particularly well marked in *Desmoteuthis*. All these venous sacs are situated to the right of the mid-intestine (*int.*) and carry the venous blood to the branchial hearts through the long branchial arteries. The branchial arteries bear venous sacs in a large part before they open into the branchial hearts; there are also smaller sacs at the opening of the pallial vein. The branchial hearts have the normal oval or pear-shaped form and have only a small appendage which is visible only if they are folded over and examined from the dorsal side. The blood passes in the normal way from the branchial hearts to the gills. The gills are sickle-shaped in lateral view, their concavity facing the head. They are 10 mm long and bear about 21 dense branchial lamellae on each side.

The efferent branchial vein is also long and forms a curve which is slightly convex anteriorly. Both branchial veins (Figures 12, 14, *v. branch.*) open in the heart without dilatation or thickening of the walls. The heart (Figure 12, *c.*, Figure 14) covers the beginning of the right hepato-pancreatic duct and extends to near the bifurcation of the two branchial arteries; toward the branchial veins it forms broad processes, so that it has a slightly rhomboidal form with concave lateral surfaces. The cephalic aorta (*a. ceph.*) is slightly spindle-shaped where it leaves the heart. It is situated distal to the large anterior pancreatic appendages and sends off at first the dorsal artery (Figure 12, *a. dors.*) and then the hepatic artery (*a. hep*). The cephalic aorta extends at first on the right of the esophagus and passes then gradually to its dorsal side. The posterior artery (*a. post.*) originates on the ventral apex of the heart and continues as usual on the ventral wall.

The other inner organs do not differ much from the normal condition and only the **genital conditions** will briefly be described. The specimen is a female with markedly retarded genitalia. The ovary (Figure 12, *ov.*) is visible as a transparent gland on the dorsal side of the stomach in the live animal; it is elongate and extends over the posterior half of the stomach. The gonoducts were not visible from the outside; they were revealed only upon closer examination, forming small ducts behind the branchial hearts. It is therefore hardly surprising that no trace of nidamental glands could be discovered.

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Luminous Organs

(Plate LX, Figures 18–21)

The narrow ventral side of the oval eye bears two very large luminous organs (Plate LIV, Figures 7, 8). Since these organs have never been described for *Desmoteuthis* nor for other Cranchiidae that have no cartilaginous ridges on the mantle, I examined them in detail in a series of sections; the organs of *Desmoteuthis* gave valuable information because of their excellent preservation. The form and size of these organs were described above (p. 280). The organs of the preserved specimen had a yellowish sheen and were distinctly visible after removal of the lid.

Longitudinal sections of the eye (Plate LX, Figure 18) show that the luminous bodies (*phot.*) with their reflectors are facing in opposite directions: those of the anterior organ (*luc. ant.*) are situated distally and those of the posterior organ (*luc. post.*), proximally. The large fibrous systems (*str.*), which extend from the luminous bodies and may be lenses, thus face each other; however, they are not contiguous but separated by a large pad of connective tissue (*pulv.*).

The luminous bodies (*phot.*) of both organs are sickle-shaped and flattened. The longitudinal section shows that the luminous body of the anterior organ is thicker than that of the posterior organ. The cells of the luminous body are of the same form in the two organs. The luminous cells are nearly polyhedral at the bottom of the organ (Figure 21) and slender near the fibrous systems (Figure 19, *phot.*). The cells usually overlap each other like shingles and have indented or serrate margins in all the places where they meet the vascular capillaries. The nuclei of the more deeply situated cells are rounded or oval, those of the peripheral cells are drawn out to an oval (Figure 19). The chromatin is generally fine and uniformly distributed, though near the margins of the nucleus it may pile up a little. Preparations stained with carmine or hemalum show the cells to be homogeneous but having a slight longitudinal striation at some points. Staining with iron hematoxylin produces a very peculiar structure which I have not found in any other luminous cells: the entire luminous body assumes a blackish shade. This is caused by the fact that each cell contains a bundle of fibers (Figure 20) which extend either parallel or converge toward the tapering end of the cell, like rays; in the deeper cells the fibers are stacked loosely, in the peripheral cells, however, they lie so densely that the cells appear almost uniformly black. The nuclei remain pale even when stained with iron hematoxylin; they are mostly situated at the end of the cell and are not covered with fibers. These inlaid fibers usually extend along the longitudinal axis of the luminous body, though those of adjacent cells may cross each other.

365 I do not know the physiological function of these fibers. They are certainly not cuticular secretions of the luminous cells of the type comprising the "striated bodies" observed in the organs of Euphausiidae.

The space between the peripheral luminous cells is filled by large fibrous systems (*str.*) which extend in regular curves to the periphery and are covered there by a thin ectodermal epithelium. These systems consist of long, bandlike fibers the margin of which may form an undulate membrane (Figure 19, *str.*). Their nuclei (*nu. str.*) are very elongate; they are situated at the periphery of the luminous body between the oval nuclei of the luminous cells, from which they are easily distinguished. The large fibrous system of the posterior organ seemed to enclose in its center a lacunar space which separates the curved peripheral fibers from the parallel ones near the eye cartilage (*cart.*).

The luminous bodies of both organs are surrounded by reflectors (*refl.*) which are thick at the bottom and rapidly flatten toward the periphery. The reflectors consist of undulate lamellae with oblong oval nuclei. The lamellae become looser toward the periphery and are only indistinctly delimited from the fibrous system which is apparently a lens.

The organs have a rich vascular supply. Thick vessels pass at bottom of the iris in the area of the anterior organ (*s. ven.*), extend straight across the reflector and form the capillary network. The long oval nuclei of the blood vessels (Figure 21, *nu. cap.*) stain slightly more intensively than those of the luminous cells.

A brief description of the structures situated in the neighborhood of the luminous organs is in order.

The iris (*ir.*) surrounds the anterior organ. It consists of the systems of lamellae which have fibers with an undulate margin and long, oval nuclei and are usually present in those places that reveal a golden or silvery sheen. Between the two luminous organs there is a thick pad (*pulv.*); this, again, consists of loose systems of lamellae that are irregularly scattered and have oval nuclei. Scattered pale, bandlike fibers are sometimes also present. The ciliary muscle (*mu. cil.*) is situated at the bottom of this pad, near the insertion of the ciliary (epithelial) body (*c. cil.*). This muscle consists of radial fibers which are inserted at the anterior end of the eye cartilage and sometimes also penetrate into the intermediate pad.

Measurements

Dorsal length of mantle	77 mm
Length of head (dorsal to base of arms)	6 mm
Width of head	18 mm
Length of fins	15 mm
Width of both fins	16 mm
Length of 1st arm	13 mm
Length of 2nd arm	16 mm
Length of 3rd arm	19 mm
Length of 4th arm	13 mm
Length of tentacle	25 mm
Length of club	7 mm

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Taonius Steenstrup, 1861

Taonius pavo Lesueur

Loligo pavo Lesueur, 1821, *Journ. Ac. Nat. Sc. Philad.*, Vol. II, p. 11, Plate.

Loligopsis pavo Férussac and d'Orbigny, 1835–48, *Céph. acét.*, p. 321; *Calmar* (*Loligo*), Plate VI; *Loligopsis*, Plate IV, Figures 1–8.

Taonius pavo Steenstrup, 1861, *Overblik Cranchiaeformes*, pp. 70, 84.

Desmoteuthis hyperborea Verrill, 1881, *N. Am. Ceph.*, p. 302, Plate XXVII, Figures 1, 2; Plate XXXIX, Figure 1.

Taonius pavo Hoyle, 1884, *On Loligopsis*, p. 318.

Loligopsis pavo Rochebrune, 1884, *Loligopsidae*, p. 5.

?Phasmatopsis cymoctypus Rochebrune, 1884, *ibid.*, p. 9, Plate I, Figures 1–4.

Taonius pavo Hoyle, 1886, *Ceph. "Challenger"*, p. 45.

Taonius pavo Pfeffer, 1900, *Syn. Oeg. Ceph.*, p. 191.

Taonius pavo Joubin, 1900, *Camp. Sc. Monaco*, Fasc. XVII, p. 106; Plates VIII, IX, X, Figures 7–9; Plate XV, Figure 16.

Taonius pavo Richard, 1903, *Bull. Soc. Zool. Fr.*, Vol. XXVIII, p. 63.

Taonius pavo Joubin, 1903, *C. R. Acad. Paris*, Vol. 136, p. 100.

Taonius Chun, 1906, *Syst. d. Cranchien*, p. 85.

In the stomach of a gray albatross (*Diomedea fuliginosa*), killed at the edge of the antarctic ice (Station 146, 50° 52′ S, 43° 0′ E) the mantle of a cephalopod was found; the mantle was 188 mm long and showed distinctly the characters of *Taonius pavo.* The long, half-oval fin, the pointed posterior end of the body that projects beyond the fins, and the well-preserved, purple brown pigmentation unequivocally point to *T. pavo.*

This is of interest because it is the first record of this species from the Antarctic. One should not be surprised to find that typical deepwater forms may occur at the surface, especially in cold currents. In my opinion, it is precisely the vicinity of icebergs that favors the ascent of deep-water forms. Since six sevenths of an iceberg lie underwater, an iceberg 50–60 m high is submerged to more than 300 m. The constant heavy storms, which often whip the surf over the plateau of the iceberg on its weather side, give rise to a sucking effect on its lee side, resulting not only in an influx of surface water but also in the upwelling of deep water, especially in the case of broad icebergs. The constant flights of shearwaters and albatrosses around icebergs suggest an abundance of organisms on the surface, caused not only by the surf but also by the sucking effect of the wind in the lee of the iceberg.

Commenting on the old illustration by Lesueur which perfectly points up the character of the species, I would only add that from the funnel there projects a stem with ramified appendages which end in small clusters. Lesueur considers the appendages as a torn-out oviduct. I find, however, that it rather resembles the genital cluster of *Physalia*, which had somehow become entangled with the specimen.

367 ## *Corynomma* Chun, 1906

Corynomma speculator Chun
(Plate LV; Plate LX, Figures 13–16)

nov. gen. *Cranchiidarum* Chun, 1903, *Tiefen d. Weltmeeres*, 2nd ed., p. 578, Figure.
nov. gen. *Cranchiidarum* Chun, 1903, *Leuchtorg. u. Augen Ceph.*, p. 83, Figure 9; p. 84, Figure 10.
Corynomma speculator Chun, 1906, *Syst. d. Cranchien*, p. 85.
Liguriella podophthalma Issel, 1908, *Cef.* "*Liguria*", p. 228, Plate X, Figure 45; Plate XI, Figures 45–56.

Locality: Station 32: Canaries Current, 24°43′ N, 17°1′ W. Vertical net to 2,000 m.
Station 237: Branch of the Indian South Equatorial Current, 4°45′ S, 48°58′ E. Vertical net to 2,000 m—One specimen.

Describing the genus *Corynomma*, we introduce the first of those peculiar Cranchiidae which have stalked eyes and a head that is produced into a "head pillar" from the base of the eye stalks.

The genus *Corynomma* has a fleshy, cylindrical body with small fins which do not project beyond its posterior end. It also has a slender head pillar and long, slender eye stalks with ovoid eyes. The arms are small, while the strong tentacles are very long and have a club with a well-developed keel. The tentacle stalks bear suckers in 2 or 4 rows almost their whole length.

Liguriella podophthalma, described by Issel (1908), is apparently identical with this species. Issel's specimen is slightly smaller than the younger specimens in my collection; it is also severely damaged: the eyes are flayed and the mantle shows wrinkles along the gladius; such wrinkles (called tubercles by Issel) are often found in worn-down forms of Cranchiidae. Otherwise the form, and especially the characteristic form of the tentacles with their quadriserial suckers—the typical arrangement in younger specimens—is in good agreement with *Corynomma speculator*.

The **mantle** has the form of a slender chalice; its anterior margin is not narrowed and the posterior end is slightly pointed. The 3 points of fusion of the mantle margin are not distinct; the ratio of width to length is about 1 : 3. The narrow gladius shines through on the dorsal side; it widens posteriorly into a spoon anterior to the base of the small fins. A specimen from the Atlantic and one from the Indian Ocean have a dorsal mantle length of 11 mm; a larger, severely damaged specimen of the German Antarctic Expedition is nearly 3 times as long. The fins of the larger specimen are 6.5 mm long at the dorsal base
368 and 5 mm wide. They are bluntly quadrangular—almost semicircular in the larger specimen. Along their base on the cone of the gladius the fins diverge at an acute angle; their posterior margin projects only slightly beyond the posterior end of the body.

The **funnel** is moderately large and does not reach the base of the arms. The middle (dorsal) part of the funnel organ (Text Figure 32a; p. 245) is heart- or shovel-shaped and shows a weak median ridge bordered by two sickle-shaped lateral swellings. The lateral (ventral) parts are kidney-shaped.

The head extends into a long pyramidal head pillar which tapers slightly toward the base of the arms (Plate LV, Figure 3). It is gelatinous, like the two eye stalks, so that the brain, the nerves

originating from it and the esophagus are visible through it. The eye stalks are not movable, relatively slender and long, and slightly curved in one specimen (Text Figure 11, p. 21). The body-head cavity continues into the inside of the eye stalks in whose center passes the unusually long optic nerve, which swells into a large optic ganglion (*g. opt.*) below the eye. The optic ganglion is more or less kidney-shaped because a groove which begins at the entrance of the optic nerve divides it partly into halves.

Two smaller nerves extend dorsally and ventrally in the gelatinous wall of the eye stalk. One of them originates on the posterior lateral part of the brain at the level of the optic nerve, the other on the anterior ventral side of the brain. These two nerves correspond to the nervus ophthalmicus superior (*n. ophth. sup.*) and inferior (*n. ophth. inf.*) of CHÉRON. Like the optic nerve, both are covered laterally by a stripe of ganglionic cells and are accompanied by a blood vessel. These nerves penetrate into the tissue which forms a ring in the space between the optic ganglion and eyeball. This tissue corresponds in its position exactly to the so-called white body of the eye of Cephalopoda; the ophthalmic nerves pass through this tissue in this species before they branch at the lateral walls of the eyeball.

The **eye** is laterally compressed and therefore ovoid. There is a pad of connective tissue fibers on its ventral pole on one side (CHUN, 1903, *Leuchtorgane und Augen*, p. 84, Figure 10). The eye of the larger specimen collected by the Antarctic Expedition which was 4 mm long and not so markedly laterally compressed as in the younger specimens, shows that this pad gives rise to a large luminous organ which covers the ventral side. But even in the larger specimen, the organ is apparently not fully developed, though one can make it out distinctly, set off against the dark eyeball.

There are also chromatophores on the eyeball. One of them is very large and covers the dorsal side of the eye; two smaller chromatophores are situated on the ventral side. The median section shows that the lens is not situated in the main axis but is slightly displaced ventrally (CHUN, 1903, Figure 10). The retina shows a continuous lengthening of the rods toward the dorsal surface, where it ends at a considerable distance from the epithelial body.

369 The stalked eye is of bilateral symmetrical, not radial form. The bilateral symmetry is expressed not only in the one-sided ventral position of the pad but also in the form of the iris, which originates dorsally at the peak of the pad but thickens ventrally where it projects onto the middle of the epithelial body.

I did not find an olfactory tubercle; possibly it is not yet developed; it should be situated behind the luminous organ, where I found a torn-off process in the larger eye.

The **arms** of the younger specimens are very undeveloped, except for the tentacles; nor are they more than moderately developed in the older specimen. The arm formula is 3, 4, 2, 1. The 3rd arms are 8 mm long, the 1st arms only 4 mm. The protective membranes are only weakly indicated; swimming membranes are absent except on the 3rd arms, where they form very weak keels. All arms bear the usual biserial suckers with barely distinguishable denticles.

The **tentacles** are very large, compared to the arms. Those of the large specimen are 36 mm long, of which the club occupies 6 mm. The stalks are rounded proximally and their inner side gradually flattens distally. Nearly two thirds of the stalk are covered with small suckers which become gradually larger toward the club (Plate LV, Figure 7). The suckers show a distinct arrangement in 4 rows in the younger specimens but they form a biserial alternating pattern in the older specimen (Figure 9). This apparent biserial arrangement is caused by the oblique position of the rows of 4 suckers (Text Figure 31, p. 244).

The club passes gradually into the stalk and is curved dorsally at its tip, like a chamois horn. The suckers on the stalk are arranged in the usual rows of 4; their distal margin bears sharp denticles, of which the median ones are larger than the lateral ones. There are 6–8 denticles on the larger suckers. The protec-

tive membranes are large on the convex ventral side and have regularly situated muscular supports; on the concave side they are distinct, too, but are narrower and border directly on the suckers. Characteristic for this genus is a large, broad keel which extends almost along the whole club and is displaced dorsally at the tip, where it forms a high comb.

The specimens are transparent in life and show an only weak pigmentation by chromatophores. The mantle bears sparse chromatophores in the form of brownish spots on the dorsal and ventral side. The head pillar showed a single dorsal chromatophore at the level of the brain and two large chromatophores at the dorsal side of the eyeball. Only the stalks of the tentacles are more strongly pigmented: their outer side is covered with large chromatophores which form 2 rows on the club (Figure 8).

370

Inner Organization

The inner organization reminds one of the simple characters of the Chiroteuthidae; particularly so, the **intestinal tract,** which has the same shape in the younger and in the large specimen. The esophagus is widened slightly where it opens into a large sinus which borders on the dorsal posterior side of the liver. The mid-intestine begins ventral to this sinus. The small caecum opens into the same sinus close to the liver and is situated at a large distance opposite the opening of the esophagus. The caecum is only indistinctly divided; its anterior part contains spiral folds. A broad constriction divides the sinus from the sac-shaped stomach, which does not show a division into 2 or 3 parts. The stomach is uniformly thin-walled; in the larger specimen it has a ring-shaped thickened area on the left and right side. A short, broad ligament connects the end of the stomach with the posterior end of the body. The mid-intestine and rectum ascend as usual anteriorly on the posterior side of the liver. The anal appendages are large and slightly sickle-shaped, with an almost straight outer margin and a convex inner margin.

The relatively large liver has a shining sheath. The ducts which extend from the liver are covered their whole length by large pancreatic glands which are divided into an anterior and a posterior part. The hepato-pancreatic ducts open into the caecum, which is situated close to the liver so that the posterior pancreatic glands lie almost horizontally contiguous to the heart, on the anterior wall of the large gastric sinus.

The **vascular system** shows the normal condition. The vena cava forms a wide curve on the right side around the liver and opens into a venous sac which receives the small sac of the hepatic vein and both sacs at the beginning of the branchial arteries. The branchial arteries form a loop in the small and large specimens; in front of the oval branchial hearts they bear a small venous sac which also receives the abdominal vein from behind. The gills are short and thick also in the large specimen; they are 5 mm long. The branchial vein which extends from them follows the curvature of the branchial artery and opens without dilatation in the spindle-shaped heart, which is situated on the right side behind the liver. From the heart originates the cephalic aorta, which also extends on the right side near the esophagus and behind the dorsal apex of the liver.

As for the condition of the other organs, I would note only that both openings of the renal sacs are rounded and distinct. The genitals, even those of the larger specimen, were as yet very retarded, so that I was unable to gain more information on these organs.

371 ## Ventral Luminous Organs

There is a peculiar condition which of all the Cranchiidae I found only in the genus *Corynomma.* Inspection of the ventral apex of the liver showed an ear-shaped pattern near the rectum which covers the ink sac below it (Plate LX, Figure 13). I therefore made longitudinal sections (parallel to the median plane) of one half of the apex of the liver and horizontal sections of the other half (perpendicular to the median plane). To my surprise, it became evident that *Corynomma* has two large luminous organs, embedded deep in the liver. That they are, indeed, luminous organs is shown by the structure of the luminous body and by the presence of a reflector. In front of the luminous body there is a gelatinous mass. A pigmented layer is absent and is replaced by the ink sac.

The two organs (Plate LX, Figures 14–16) lie symmetrically on the ink sac and are about 0.8 mm long. They are nearly oval in longitudinal section (Figure 14), almost spherical in horizontal section. They cause a deep invagination of the ink sac, so that the latter describes a narrow slit around the luminous body (Figures 15, 16, *res.*).

The luminous body (*phot.*) is nearly crescent-shaped and has a concave outer margin. The luminous cells are polyhedral and have rounded corners which leave intervals in which capillaries pass. The cells nearer to the outer margin are smaller, more rounded, and stain more strongly. The nuclei are small, oval or rounded, with numerous chromatin granules. The cells have a finely granulate plasma and a membrane which is so thin that the boundary between two cells is often indistinct. The whole luminous body contains numerous blood vessels which apparently penetrate from the concave outer side. The nuclei of the capillaries differ distinctly from those of the luminous cells; they are long, oval, flat, often of irregular form. The nuclei of the capillaries appear as straight or curved lines from the narrow side.

The luminous body is surrounded toward the ink sac by a thick **reflector** (*refl.*) which consists of two layers: an irregular outer layer of fibers with long nuclei and an inner layer of granulate cells, resembling those in the anal organs of *Pterygioteuthis.* The nuclei of these cells are oval, nearly rounded at the bottom of the reflector, and are surrounded by refractile flakes.

The luminous body borders on the subcutaneous connective tissue which encloses a large gelatinous body (*gel.*) which is perhaps a lens. The margin of this peculiar formation sometimes shows wide bands of fibers with nuclei and rounded granulate cells which often contain two nuclei, rarely several. These cells stain intensively and sometimes form nests scattered throughout the gelatinous body. The gelatinous body is surrounded by subcutaneous connective tissue which also isolates it from the fibrous layer of the reflector and forms a thin layer between the gelatinous body and the luminous body.
372 The subcutaneous connective tissue forms ear-shaped thickenings on both sides of the rectum (Figure 13) which sometimes seem to extend over the other part of the subcutaneous connective tissue.

Measurements

	Larger Specimen	Smaller Specimen (Station 237)
Dorsal length of mantle ca.	32 mm	11 mm
Length of head pillar	4.5 mm	3.5 mm
Eye stalk (to eyeball)	4.5 mm	
Length of eye	4 mm	2 mm
Length of base of fins	6.5 mm	
Width of fin	5 mm	

Measurements (contd.)	Larger Specimen
Length of 1st arm	4 mm
Length of 2nd arm	6 mm
Length of 3rd arm	8 mm
Length of 4th arm	7 mm
Length of tentacle	36 mm
Length of club	6 mm

Crystalloteuthis Chun

Crystalloteuthis glacialis Chun
(Plate LIII, Figures 2–9; Plate LIV, Figure 18)

Cranchiidarum n. gen. Chun, 1903, *Tiefen d. Weltmeeres*, 2nd ed., p. 232, Figure.
Crystalloteuthis glacialis Chun, 1906, *Syst. d. Cranchien*, p. 85.

Locality: Station 145: Antarctic Drift Current, 59°16′ S, 40°13′ E. Vertical net to 1,500 m—One specimen.

One medium-sized specimen of *Crystalloteuthis* was caught in the Antarctic. This peculiar genus is apparently a member of Cranchiidae that is intermediate between those Cranchiidae that have cartilaginous tubercles on the ridges of fusion of the mantle and those that have stalked eyes. *Crystalloteuthis* has characteristic cartilaginous tubercles at the points of fusion of the mantle but otherwise resembles the Cranchiidae with stalked eyes.

The body is fleshy, spindle-shaped, with a pointed posterior end which projects beyond the small fins. The eyes are oval and have short, thick stalks. The arms are moderately developed, while the tentacles are large and have an only slightly widened club without a keel.

The spindle-shaped **mantle** ends posteriorly in a pointed tip which projects slightly beyond
373 the fins. The dorsal length of the mantle, which is the same as that of the gladius, is 35 mm. The fins are considerably longer than wide and form together an oval disc 6 mm long and about 5.5 mm wide. The gladius is 1 mm wide between the fins; elsewhere it forms a thin rod which extends to the dorsal margin of the mantle, where it widens slightly. Especially characteristic are the **cartilaginous tubercles** on the mantle margin. The ventral points of fusion of the mantle bear two tubercles (Figure 8) of which the outer one is branched like antlers with 5 processes, the inner one with only two processes. The dorsal point of fusion also bears two tubercles; they are situated symmetrically near the end of the gladius and have about 3 blunt processes (Figure 9). These tubercles are so characteristic for the genus that they constitute a reliable clue for the recognition of any specimen found by future expeditions. The head is short and characterized by a short, plump head pillar.

The **eyes** are relatively large and have short, thick stalks. They are slightly contracted in the preserved specimen (Figure 3); they protruded more in the live animal from which Figure 2 was drawn. The eyes are oval, 4.2 mm long and 3 mm wide. The eyelids of the preserved specimen covered the whole eyes, leaving only a small opening of irregular form, as shown in Figure 7. Removal of this lid fold (Figure 7, right eye) shows a light ventral disc which comprises the large luminous organ. It consists of a large, crescent-shaped anterior part, contiguous to the relatively large lens, and a sickle-shaped posterior part which surrounds the anterior part.

An olfactory tubercle could not be found. The **funnel** is large and extends to the base of the ventral arms; its ventral lamella, which is fused laterally with the mantle, projects far into the mantle cavity (Figure 7). The funnel organ (Text Figure 32 c, p. 245) consists of two oval or blunt rectangular lateral parts and a single part, behind which the vena cava is seen. The single part is triangular and extends posteriorly in two crescent-shaped lateral areas. A lanceolate process is present in the middle; the lateral areas bear short, conical tubercles.

The **arms** (Figure 4) differ only little in length. The arm formula is 3, 4, 2, 1; the 3rd and 4th arms are of about equal length, i.e. 7 mm, while the 1st arms are 5 mm long. The arms bear the usual biserial suckers—14 pairs on the 2nd and 15 on the 3rd arms. The protective membranes are moderately developed; swimming membranes are absent.

The **tentacles** are large (Figures 5, 6) and the club is only slightly widened. The stalks have a median groove and small, alternating, biserial, stalked suckers almost to the base. There are about 26 pairs of suckers. They are arranged in oblique rows of 4 that become increasingly distinct toward the club, gradually passing into the rows of 4 suckers on the club itself. The latter are densely arranged; the
374 suckers in the middle are larger than the distal or proximal suckers and those of the median rows are slightly larger than those of the marginal rows. The protective membranes are of the same form and weakly developed (Figure 5); there is no trace of a keel (swimming membrane). In view of the conditions on the club of *Teuthowenia* (described hereafter), it is possible that a swimming membrane develops at the time of sexual maturation.

The specimen was in good condition and rather transparent in life; the liver, ink sac and a part of the intestinal tract were visible distinctly through the mantle. The **coloration** is not vivid and is caused by reddish chromatophores which are regularly distributed on the dorsal and ventral side of the mantle but are not arranged in distinct transverse rows. The head pillar bears 3 large chromatophores, the eye stalks and lid membrane a few moderately large chromatophores, but there are none on the arms; the outer side of the tentacles bears large chromatophores that are arranged in one row, passing into a two-row arrangement on the club.

Inner Organization

(Plate LIV, Figure 18)

The inner organization, especially the formation of the intestinal tract, gives valuable information on the relationships in the Cranchiidae.

INTESTINAL TRACT

The esophagus (*oes.*) extends obliquely toward the ventral side and shows a ring-shaped swelling where it reaches the liver, caused by the ampulla of the cephalic vein which leaves the esophagus at this point. The esophagus opens in a sack-shaped sinus (*st.'*) on the left side of which the small caecum (*st. coec.*) is situated. The stomach is sharply delimited at the point where it opens into the common sinus. It consists of a funnel-shaped anterior part (*st. str.*) with strong longitudinal folds, and a large sac (*st.*) with thin walls, which extends almost to the posterior end of the body. A ligament (*lig. g. g.*) connects the end of the sac with the tip of the gladius. The mid-intestine extends on the left side below the liver. The rectum is not sharply delimited from the mid-intestine; it bears two lanceolate anal appendages (*app. an.*) which are thin-walled lobes of equal size situated on the keel.

The spindle-shaped liver (*hep.*) is almost perpendicular to the longitudinal axis of the body and has a truncate ventral end. The ink sac (*atr.*) is small; its efferent duct, which opens in the anus, is distinct. The hepatic ducts extend from the posterior third of the liver; they bear large pancreatic glands from their base (*pancr.*). The hepatic ducts are markedly asymmetrical, the left appendages being much
375 larger than the right ones. Otherwise they resemble those of *Desmoteuthis*, inasmuch as the pancreatic follicles cover their entire length and decrease in size to the point where the ducts open into the caecum. The largest follicles lie in front of the heart and the aorta and are mulberry-shaped. The relatively large gastric ganglion (*g. gastr.*) is situated near the opening of the right hepato-pancreatic duct.

VASCULAR SYSTEM

The vena cava (*v. c.*) extends straight from the posterior margin of the single part of the funnel organ to the anterior third of the liver. The abdominal wall extends from this point like a ligament (*lig. an.*) to the anus, while the vena cava curves around the right side of the liver and opens into the large venous appendages which resemble those of *Desmoteuthis*; they are situated to the right of the mid-intestine. The drawing distinctly shows the sacs of the hepatic veins (*sacc. v. ant.*) and the sac of the cephalic and the gastric vein (*sacc. v. post.*) that is confluent with the vena cava. The cephalic vein widens into an ampulla (*amp. v.*) which completely surrounds the esophagus before leaving it and passing toward the venous sac. The branchial arteries (*a. branch.*) are long, not markedly curved anteriorly and bear venous appendages close to the branchial hearts. The oval branchial hearts have a very small, knoblike appendage on the dorsal side. The branchial veins (*v. branch.*) are slender and extend parallel to the branchial arteries before they enter the spindle-shaped heart; the latter is contiguous with the posterior ventral side of the liver. The main vessels that extend from the heart are the posterior artery and the cephalic aorta (*a. ceph.*); the latter has a spindle-shaped dilatation at the base.

The **renal sac** is of normal form and has distinct openings (*ur.*) which form slits on an oval papilla. The chimney-shaped pori interni were also distinctly visible through the renal sacs. The gills resemble those of *Teuthowenia*.

The **body cavity** is large and divided anteriorly into halves by a median septum. The septum is apparently interrupted near the liver, probably torn. It forms a slightly roof-shaped widening (*diaphr.*) at the dorsal lateral margin of the liver; the dorsal vein (*v. dors.*) and dorsal artery pass on the crest of the septum.

All other conditions are typical for the family. The funnel depressor is transformed into a muscle lamella which is fused with the mantle, and as already mentioned in the description of the funnel, the ventral margin of the funnel (Plate LIII, Figure 7) and the collaris are fused with the mantle.

The small, retarded genital gland (Figure 18, *gen.*) is situated at the dorsal side of the stomach in front of the gastro-genital ligament.

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Measurements

Dorsal length of mantle	35 mm
Maximal width of mantle	15 mm
Length of dorsal base of fins	6 mm
Width of both fins	5.5 mm

Length of head pillar	4 mm
Length of eye and eye stalk	5 mm
Length of eye	4.2 mm
Width of eye	3 mm
Length of 1st arm	5 mm
Length of 2nd arm	6 mm
Length of 3rd arm	7 mm
Length of 4th arm	7 mm
Length of left tentacle	24 mm

Teuthowenia Chun

Cranchia subg. *Owenia megalops* Prosch, 1847, *Nogle nye Cephalop.*, p. 71, Plate, Figures 4–7
Cranchia megalops Steenstrup, 1861, *Overblik Cranchiaeformes*, p. 9.
Cranchia megalops Hoyle, 1886, *Rep. "Challenger"*, p. 44.
Owenia megalops Pfeffer, 1900, *Syn. Oeg. Ceph.*, p. 193.
Owenia Chun, 1906, *Syst. d. Cranchien*, p. 85.
Cranchia megalops Hoyle, 1909, *Cat. rec. Ceph.*, 2nd Suppl., p. 276.

Teuthowenia antarctica Chun
(Plate LVI, Figures 1–5; Plate LVII, Figures 3–7)

Owenia n.sp. Chun, 1903, *Tiefen d. Weltmeeres*, 2nd ed., p. 232, Figure.

Locality: Station 136: Antarctic Drift Current, 55°57′ S, 16°14′ E. Vertical net to 2,000 m—One specimen.

Prosch (1847, p. 71) described a small species as *Cranchia* subgenus *Owenia megalops* from the northern current near Greenland. Steenstrup and Hoyle place this species in the genus *Cranchia*. Pfeffer raised the subgenus *Owenia* to the rank of a new genus. Since this name is preoccupied, I propose the name *Teuthowenia*. A specimen collected by the Deep-Sea Expedition in the Antarctic at the border of the drift ice closely resembles that described by Prosch. The description of Prosch is insufficient and I therefore refer to Pfeffer's diagnosis, which stresses the presence of 4 rows of suckers on the entire tentacle stalk. Our specimen, however, has only two rows (Plate LVII, Figure 4); further material may show whether this is a specific difference. In the meantime, I consider the southern form as a new species, *T. antarctica*. Four severely damaged specimens caught by the Antarctic Expedition near the surface in the southern Indian Ocean (on 14 May 1903) are apparently identical with the southern form. These specimens were as large as the antarctic specimen, or slightly smaller. I confine their description to the points of relevance for the diagnosis.

377 The following is characteristic for the genus *Teuthowenia*: the body is fleshy and sac-shaped; the fins are very small, hardly wider than long, and project slightly beyond the posterior end of the body; the eyes are oval and have short, plump stalks; one luminous organ is present on the ventral side of the eyeball; the head pillar is short and wide; the arms are very small; the tentacles are large and covered with suckers almost to the base; the club is only slightly widened and bears a distinct keel and wide protective membranes in older specimens.

The **mantle** is sac-shaped, membranous, only slightly narrowed at the anterior margin. The antarctic specimen has a mantle length of 13 mm. The mantle of the live animal was semitransparent and covered with brownish chromatophores which showed no distinct arrangement in transverse rows. The fins are slightly retracted and barely project to the outside. A specimen caught by the Antarctic Expedition had better preserved fins; their width measured 3 mm, and 2.8 mm at the dorsal base. The fins are situated on the lateral margins of the gladius, which widens abruptly at the anterior margin of the fins and then tapers to a pointed apex at the level of the posterior margin of the fins. The funnel is large; it projected beyond the base of the tentacles in the live specimen. The funnel organ consists of two oval ventral parts and a single part resembling a hat with a wide brim.

The oval **eyes** (Plate LVI, Figures 4, 5) are relatively large and have plump stalks which are filled almost entirely by the optic ganglion, so that only a small part of the optic nerve is visible. The iris of the live animal had a silvery sheen and the interior of the eye was black. On the ventral side of the eye is a large luminous organ which extends to the iris. I was unable to find an olfactory tubercle.

The **arms** (Plate LVII, Figure 5) are very small, hardly more than 1 mm long. They are better developed in a specimen of the Antarctic Expedition, in which the 3rd arms were almost 3.5 mm long. The arm formula of this latter specimen is 3, 4, 2, 1. Protective or swimming membranes are absent.

The **tentacles** (Plate LVII, Figures 3, 4) are very strongly developed and slightly longer than the body. They are cylindrical at the base, then gradually flatten on the inner side and are only indistinctly delimited from the club. As stressed by Prosch, the tentacles bear small, paired suckers with long stalks almost to the base. There were 21 pairs of suckers on the left tentacle of the antarctic specimen; they showed the already described alternating arrangement near the club. The club bears small stalked suckers in rows of four. The distal margin of these suckers bears 4 blunt denticles; the larger suckers show two additional denticles and some developing ones. The club of the antarctic specimen was smooth and there were no protective membranes nor a keel, but in two specimens of the Antarctic Expedition the protective membranes and a relatively large keel (swimming membrane) at the distal end were dis-
378 tinctly developed. The tip of the club showed furthermore the usual dorsal curvature into which the keel was displaced, and a marked widening of the ventral protective membrane and its distinct muscular supports.

The live animal was semitransparent and the brownish-red liver with its shining sheath was clearly visible. The pigmentation was weak on the mantle but more intense on the head. Funnel and eye stalks bear large chromatophores; two large chromatophores cover the dorsal side of the eyeball. The dorsal arms are slightly pigmented; the tentacles of the live animal were bright brownish, due to large chromatophores arranged in a row (Plate LVII, Figure 3).

Inner Organization
(Plate LVII, Figures 6, 7)

The data published by Prosch on the inner structure of *Owenia* are so aphoristic that a brief description is indicated, especially in view of certain erroneous interpretations. The specimen was cleared in oil of cloves and later I made preparations to get insight into certain points. Opening of the mantle cavity shows that the funnel depressors are transformed into a lamella which is fused with the lateral walls of the mantle, and its free posterior margin surrounds the gills (Figure 7).

Intestinal tract. The esophagus leaves the dorsal side at the level of the stellate ganglia (*g. stell.*) and ascends obliquely posteriorly, where it enters a small sinus. From this sinus there begins the sac-

shaped stomach (*st.*), which extends almost to the posterior end of the body. Situated on the stomach is the small caecum (*st. coec.*), with its spiral folds. The mid-intestine (*int.*) is very wide; it ascends to the lower side of the liver and passes into the slightly narrower rectum which opens between the anal lips (*an.*) with their spatulate anal appendages which are narrow and symmetrical. The liver (*hep.*) is relatively short and wide; it is situated almost perpendicular to the longitudinal axis of the body. On the ventral apex of the liver the small ink sac (mentioned already by PROSCH) is situated, the efferent duct of which is black. The dorsal posterior margin of the liver is covered on both sides by the very large pancreatic appendages (*pancr.*), which join to give rise to the hepato-pancreatic duct (*d. hep. pancr.*) that extends without appendages along the mid-intestine and opens in the small caecum.

Vascular system. The vena cava (*v.c.*) appears on the surface of the abdominal wall, behind the single part of the funnel organ, curves broadly around the right side of the liver and then opens into the venous sacs behind the liver. These venous sacs are small, but the branchial arteries which originate in them (Figure 7, *a. branch.*) are very thick and long; they form again venous appendages (*sacc. ven.*) anterior to the oval branchial heart. On the dorsal side of the rounded branchial heart (*c. branch.*) there is
379 the very small, knoblike appendage of the branchial heart. The gills are short and thick, with about 14 lamellae on each side. The branchial vein (*v. branch.*) is markedly thinner than the branchial artery and opens on both sides into the spindle-shaped heart. The large oval openings of the renal sacs (*ur.*) are visible in front of the heart, at the level of the pancreatic appendages.

The main characters of the inner organization are thus the small size of the caecum compared to the stomach, and the curve described by the well-developed pancreatic appendages on both sides of the liver, without continuing along the terminal part of the hepato-pancreatic duct and extending to the caecum. The vena cava opens into moderately large venous sacs, and there are well-developed branchial arteries with large venous appendages anterior to the branchial heart.

Sandalops CHUN

Sandalops melancholicus CHUN
(Plate LVI, Figures 6–8)

Sandalops melancholicus CHUN, 1906, p. 86.

The Antarctic Expedition collected two specimens of the new genus *Sandalops* with a vertical net at a depth of 1,000 m in the southern Atlantic (north-east of Tristan da Cunha). These specimens are juveniles, only 20 mm long. They differ in many points from the other genera of Cranchiidae and show some characters which certainly characterize also older specimens. A detailed description of these specimens will be given elsewhere; here I shall make only a few remarks. The mantle is fleshy, cylindrical, 11.5 mm long. The fins are small, wider than long and are situated on the lateral margins of the gladius, which has a widened, spoon-shaped posterior end (Figure 7). The peculiar sandal-shaped eyes have long, thick stalks. The head pillar is long. The arms are very small, and the relatively short tentacles are covered almost to the base with small, stalked suckers.

Inner organization. The caecum of a cleared specimen is also much smaller than the elongate, sac-shaped stomach. There are distinct pancreatic appendages which accompany the hepato-pancreatic duct to its opening in the caecum, as in *Desmoteuthis*.

380 *Toxeuma* CHUN

Toxeuma belone CHUN
(Plate LVI, Figure 10; Plate LVIII, Figures 1–5)

Cranchiidarum n. gen. CHUN, 1903, *Tiefen des Weltmeeres*, 2nd ed., p. 553, Figure.
Toxeuma belone CHUN, 1906, *Syst. d. Cranchien*, p. 86.

Locality: Station 182: Indian South Equatorial Current, 10°8′ S, 97°14′ E. Vertical net to 2,400 m—One specimen.

We collected a transparent, medium-sized cranchiid at Station 182 in the Indian Ocean, north of the Cocos Islands; its body was very slender and more distinctly arrow-shaped than in any other Cephalopoda. The genus *Toxeuma* resembles a young *Taonidium* but differs from it in the form of the eyes, head and tentacle club.

The **body** is fleshy, arrow-shaped, with a needle-shaped posterior end. The fins are long and narrow; they surround the posterior part of the body without reaching the posterior tip. The eyes are conical; the eyeball is longer than wide. The eye stalks are thick and moderately long; the head pillar is long and slender. The arms are small, the tentacles large, but shorter than the body, and have a slightly widened club and a narrow keel.

The **mantle** is spindle-shaped and has a narrowed anterior margin; its long posterior part passes into the end part of the gladius, which projects in the form of a needle. The gladius is dorsally visible as a fine cord; it slightly widens toward the dorsal corner of the mantle and in the middle of the fins and then tapers to a needle-shaped point. The gladius is 51 mm long and is posteriorly surrounded by two long, narrow fins. The fins resemble those of *Taonius* and *Taonidium*: they are 14 mm long and both together only 4 mm wide. The anterior margin of the mantle is smooth and projects only slightly at the corners. The ventral corners show short cartilaginous stripes from which extend the partly visible points of fusion of the collaris and the funnel. The funnel (Figure 3) is broad and does not project beyond the base of the eye stalks but hangs limply. The base of the eye stalks is broad, the head pillar slender, and the dorsal and ventral muscular hands are distinct (Figure 3). The eye stalks are broad, plump, and 3 mm long. The **eyes** are large and longer than wide (Plate LVI, Figure 10), in contrast to the Cranchiidae described so far. Older specimens apparently have the typical telescopic eyes. The eyes are 3 mm long
381 and 2 mm wide. The eyeball is nearly ovoid; in specimens cleared in oil of cloves it has a dark-violet pigment which contrasts sharply with its background—the broad ciliary body. The large lens protrudes hemispherically. There are two luminous organs on its posterior ventral surface, a larger sickle-shaped posterior organ and a smaller, crescent-shaped anterior organ (Figure 3). Close to the organs, a part of the eyeball is conspicuously bronze-colored. A shallow groove which divides the anterior part from the pigmented posterior part is visible in the cleared eye.

The brain and some nerves which originate from it are visible through the gelatinous eye stalks and head pillar. From the rhomboidal cerebral ganglion originate laterally the thick optic nerves, which swell into large, half-oval optic ganglia. The superior and inferior ophthalmic nerves which extend to the eyeball are also visible. An olfactory tubercle could not be demonstrated.

The **arms** (Figure 3) are moderately large; formula: 3, 4, 2, 1. The 3rd arms are 4.5 mm long, the 1st arms barely 3 mm. The arms bear the usual biserial suckers and have only weakly developed protective membranes; swimming membranes are absent.

The **tentacles** (Figures 4, 5) have a length of 19 mm, of which the club forms 2.5 mm. The

stalks are nearly cylindrical and only slightly flattened on the inner side. The stalks bear distally 10 pairs of suckers, of which the proximal ones are more widely spaced. The club is only slightly widened and its tip is dorsally somewhat curved, almost forming a sickle. The convex outer margin bears a relatively wide protective membrane (Figure 4), but that of the concave margin is weak. The swimming membrane is displaced to the concave margin and forms a weak keel. The suckers have long stalks and are arranged in rows of four. Those in the middle of the club are slightly larger and a little less regularly arranged. The distal margin of the larger suckers bears 4 denticles of which the two median ones are larger than the adjacent ones.

The body was almost completely transparent and lacked chromatophores except for two large ones, covering the distal side of the eye, and several chromatophores on the club arranged in a row; there are also scattered chromatophores on the protective membrane of the club and traces of chromatophores on the base of the head pillar.

Since I did not want to dissect the valuable specimen, I can describe the **inner organization** only as far as it was recognizable in the cleared specimen without further preparation. *Toxeuma* does not differ from the normal structure of the Cranchiidae. The esophagus widens slightly at the level of the liver; the latter is situated perpendicular to the longitudinal axis, despite the slender form of the body. The very small caecum is situated far from the liver. The unusually slender stomach has a tubular anterior part. The pancreatic appendages are compact; they are situated on the dorsal lower surface of the liver and do not extend to the caecum.

382 **Measurements**

Dorsal length of mantle (length of gladius)	51 mm
Length of fins	14 mm
Width of both fins together	4 mm
Maximum width of mantle	8 mm
Length of head pillar	4 mm
Length of eyes (main axis)	3 mm
Width of eyes	2 mm
Length of eye stalks	3 mm
Length of 1st arm	3 mm
Length of 2nd arm	3.2 mm
Length of 3rd arm	4.5 mm
Length of 4th arm	3.5 mm
Length of tentacles	19 mm
Length of club	2.5 mm

Galiteuthis JOUBIN, 1898 (*Taonidium* PFEFFER, 1900)

Galiteuthis (*Taonidium*) *suhmii* HOYLE
(Plate LIX)

Taonius suhmii HOYLE, 1885, *Narr. "Challenger" Exp.*, p. 472, Figures 173, 174.
Taonius suhmii HOYLE, 1886, *Ceph. "Challenger"*, p. 192, Plate XXXII, Figures 5–11.

Taonius richardi Joubin, 1895, *Céph. Monaco*, p. 46, Plate III, Figures 5, 6; Plate IV, Figures 3–5.
Galiteuthis armata Joubin, 1898, *Nouv. Fam. Céphalop.*, pp. 279–292, Figures 1–9.
Taonius suhmi Jatta, 1899, *Cef.* "*Vettor Pisani*", p. 27, Plate I, Figure 25 (fide Hoyle).
Taonidium suhmi Pfeffer, 1900, *Syn. Oeg. Ceph.*, p. 192.
Taonidium suhmi Chun, 1906, *Syst. d. Cranchien*, p. 86.
Taonidium pfefferi Russell, 1909, *Ceph.* "*Goldseeker*", p. 451.

Locality: Station 43: Guinea Current, 6°29′ N, 14°35′ W. Vertical net to 2,500 m—One juvenile specimen.
Station 51: Guinea Current, 0°55′ N, 4°37′ W. Vertical net to 2,500 m—One adult.

The *Challenger* Expedition discovered south of Australia two specimens of a species of Cranchiidae which was described by Hoyle (1885, p. 472, Figure 173) as *Taonius suhmii.* A specimen collected by this expedition near the African coast in the North Atlantic belongs to the same species, according to Hoyle. He described it in detail in his *Report on the Cephalopoda* (p. 192, Plate 32, Figures 5–11). Hoyle considered as *T. suhmii* also the small juvenile forms which had aroused the lively interest of Willemoes-Suhm and were later described by Lankester (1884, p. 311, Figures 1, 2) as *Procalistes suhmii*, after drawings of Suhm. I intend to prove that this juvenile form is probably not the larva of the above species; Pfeffer (1900, p. 192) created the genus *Taonidium* for this form. A specimen I sent to Pfeffer was, by his determination, also a true *Taonidium.* For reasons which will be explained below, I have come to the conclusion that the genus *Taonidium* is the juvenile form
383 of a species which Joubin (1898) described from the Mediterranean as *Galiteuthis armata.* Joubin created the new family "Cranchionychiae" for this species. In my opinion, this is a typical species of Cranchiidae which, however, differs markedly from the other forms in that part of the suckers on the club have been transformed into hooks. The generic name *Galiteuthis* having priority, the name *Taonidium* has to be sunk.

I shall provide first a brief diagnosis of the genus and then a description of the juvenile and adult forms.

The body is fleshy and ends posteriorly in a long, needle-shaped point. The long, narrow fins surround the posterior end of the body but do not project beyond it. The head is moderately long; the eyes are ovoid and have short, broad stalks. The head pillar is short and the arms are moderately developed. The tentacles are strong, shorter than the body, and have a slightly widened club that lacks a keel; in juveniles it has quadriserially arranged suckers. The suckers of the marginal rows in the middle of the club disappear in adults, while some pairs of those in the median rows are transformed into hooks. In the developed carpal zone there are adhesive knobs between the suckers. The distal part of the tentacle stalk bears alternating suckers in 2 rows.

a) Characteristics of the Juvenile Form (*Taonidium*)

The following description is based on a young specimen caught at Station 43 in the Guinea Current (Figures 3, 4). This specimen closely agrees with Hoyle's description of *Taonidium suhmii* in form and other characters.

The **mantle** has the form of a deep goblet; it has a slightly narrowed anterior margin and ends in a sharp point. The gladius is visible as a thin rod which slightly widens anteriorly, near the dorsal corner of the mantle, and has an oblong widening at the middle of the fins. The gladius and the dorsal side of the mantle are 34 mm long. The fins are situated on the widened part of the gladius. They form together an oval which is 6 mm long and 5 mm wide. Each fin is thus almost twice as long as wide.

The **funnel** is moderately large and does not project beyond the base of the eye stalks. The head is relatively narrow and the head pillar is 3.5 mm long.

The **eyes** are ovoid, large, and have short stalks; only the eyeball, with the optic ganglion, projects above the surface. The eyes are 3 mm long and 2 mm wide. The ventral side of the eyeball is slightly wider than the dorsal side. The optic ganglion, optic nerve and both ophthalmic nerves are visible through the plump eye stalk. The small, sessile olfactory tubercle is situated on the ventral side.

384 The **arms** are situated on a short, thick head pillar and are moderately large (Figure 9). The formula is 3, 4, 2, 1. The 2nd and 4th arms are of about equal size and 4 mm long. The protective membranes are well developed and have muscular supports. The protective membrane of the ventral arms broadly surrounds the base of the tentacles (Figure 8) and then continues on the 3rd arm without passing into its protective membrane. The attachment to the buccal funnel is typical for the Cranchiidae. Examination of the buccal funnel from above shows in its inside the thin outer lip and the wide, fluted inner lip (Figure 9).

The **tentacles** (Figures 6, 7) of the preserved specimen have a length of 30 mm, of which the club forms 5 mm. The tentacle stalk is round, but on the inner side, toward the distal part, it gradually flattens; it bears 28–30 pairs of stalked, alternating suckers. The stalk passes gradually into the club, which has no keel (swimming membrane) but has distinct protective membranes. The club bears 12 rows of 4 suckers. The two proximal rows later form the carpal part; between them are 5 delicate adhesive knobs. About 5 proximal pairs of suckers of the median rows are slightly larger than those of the lateral rows. There is a striking and important condition: 3 larger suckers of the median rows are transformed into small hooks and another sucker is beginning such a transformation (Figure 7).

The live animal was brightly colored. The mantle bears orange chromatophores which do not show an arrangement in distinct transverse rows. Chromatophores are also present on the head; there are two large chromatophores on the dorsal side of the eyeball. The arms are weakly pigmented, but the tentacles are strongly colored, having large chromatophores which are arranged in one row and extend along their entire length, especially along the club. The club bears also marginal chromatophores, situated on the protective membranes.

b) Adult *Galiteuthis*

The adult specimen caught in the Guinea Current (Plate LIX, Figures 1, 2) is clearly identical with that described by Joubin from the Mediterranean. The specimen was slightly damaged in the anterior part of the mantle, but the head and the posterior end are well preserved. It is only slightly smaller than Joubin's specimen. The two specimens are very similar and only those points will be described that complement the previous description.

The **mantle** forms a deep goblet with a long, pointed posterior end. The anterior margin of the mantle is only slightly narrowed and distinctly shows the 3 points of fusion. The gladius forms a thin rod which is 110 mm long and shows a widening at the dorsal corner of the mantle and another at
385 the base of the fins. The fins taper on both sides and form together a long oval; they are situated dorsally on the widened part of the gladius, which projects beyond them. The head is relatively thick and has a short head pillar which is more distinct in our specimen than in that from the Mediterranean. The thick muscular cords of the head pillar, which extend from the margin of the funnel to the arms, have been described by Joubin. The funnel does not project beyond the base of the eye stalks and is moderately developed. The eyes (Figure 11) have short, plump stalks, through which the large optic ganglion is visible. The eyes are oblong-oval. Their ventral side bears a large luminous organ which

forms an almost circular disc and consists of a smaller oval anterior part fitting into a crescent-shaped larger posterior part. Below the organ, at the level of the optic ganglion, there is the stalked olfactory tubercle (*tub. olf.*); it has a knob-shaped thickening at the end which consists of sensory epithelium. Joubin failed to mention this tubercle.

The **arms** (Figure 10) are moderately developed; the formula is 4, 3, 2, 1. The 1st arms bear 9 pairs of suckers, the following arms 10, 23 and 18 pairs, respectively. All arms also bear very small suckers at their tips, which are hardly recognizable under the magnifying lens. The protective membranes are distinctly developed and bear transverse bridges which alternate with the adjacent suckers. Swimming membranes are present only in the distal half of the arms; they form weak keels on the 3rd arms but comprise a moderately high keel on the 4th arm; this keel extends along the whole arm and broadly surrounds the tentacle at the base before it extends to the 3rd arms.

The buccal funnel is well developed and shows the conditions typical for the Cranchiidae. It is supported by 7 pillars; the attachments extend dorsally to the 1st and 2nd arms, ventrally to the 3rd and 4th arms. The buccal funnel is smooth and is covered with purple chromatophores on the outside; its inner side is slightly rugose. The outer lip is narrow and circular, the inner broader and fluted.

The **tentacles** are about 24 mm long in the preserved specimen, i.e. about half as long as the body. The tentacle stalk is rounded at the base but then flattens on the inner side and has a weak median groove in the distal part. Alternating pairs of small suckers cover almost the whole stalk, except in the proximal part; there are 26 pairs of suckers on each tentacle. The flat inner side of the stalk widens gradually toward the club; in good illumination it shows small knobs between the suckers.

The **club** (Figure 5) is 8 mm long, including the carpal part. Its outer side is rounded and has no swimming membrane (keel), but the protective membranes are well developed and continue slightly beyond the carpal part; the muscular bridges are hardly recognizable.

The inner side of the club is distinctly divided into 3 parts: it consists of a proximal carpal part, a middle part with hooks, and a sucker-bearing tips. The carpal part was different on each club. It bears 3 rows of 4 suckers on the left club, bordered proximally by a markedly oblique row of 4 small
386 suckers which forms a transition to the small suckers of the stalk. About 5 adhesive knobs are present between the suckers. One median sucker of the distal row was being transformed into a hook. On the right club (Figure 5), 4 or 5 suckers are still present, with about twelve knobs between them. Some of these knobs are probably stalks of suckers which have been lost.

That part of the club that has hooks which developed by transformation of the suckers of the median rows consists of 6 hooks on each side on the right club (Figure 5), of which the median ones are the largest; there is also a smaller distal hook in the dorsal row. The marginal suckers are completely suppressed, except for two proximal and two distal suckers. On the left club, the part having hooks also consists of 6 hooks on each side, but there is also one proximal ventral and one distal dorsal sucker; they are in the process of being transformed into hooks.

The distal part of the right club bears 4 oblique rows of 4 suckers and several very small suckers which decrease in size. The median ventral sucker of the proximal row is being transformed into a hook. The same condition is observed on the left club.

The **color**. The head and arms of the live animal were vividly colored, but on the mantle there were only a few scattered chromatophores. The dorsal side of the fins showed more numerous chromatophores, and the tip of the gladius was rust-red. The primary shade of the head is violet, set off against this color are the brownish red chromatophores—smaller ones in the area of the optic ganglion (Figure 11) and larger ones on the dorsal side of the eyes. The outer side of arms and tentacles is covered with uniserial chromatophores; on the club they are mixed with smaller ones.

According to the above data, I conclude that *Taonidium* is the juvenile form of *Galiteuthis*. The specimen of *Galiteuthis* examined is 3 times as large as *Taonidium* and accordingly shows certain differences in the relative size of the different parts. This applies particularly to the posterior end, which differs from that of the juvenile animal in the relatively narrower fins and the longer tip which projects far beyond the fins. Not only the close resemblance in the form of the body led me to the conclusion that *Taonidium* is identical with *Galiteuthis*; it is based mainly on the form of the club. In *Taonidium*, 3 pairs of suckers of the median rows of the club are already transformed into small hooks, while some adjacent suckers are undergoing such a transformation. Only *Galiteuthis* of all the Cranchiidae shows such a condition. Admittedly, there are distinct differences between the club of the adult and that of the juvenile *Galiteuthis*. In the adult form, the suckers of the marginal rows are absent in the part of the club that has hooks, while in the juvenile form they are well developed. The fact that only a few small marginal suckers persist in *Galiteuthis* may be due to a secondary loss of the other marginal suckers. A similar condition is present on the club of the Enoploteuthidae.

387 I consider the above-described differences between the juvenile and adult specimens of *Galiteuthis* to be bridged by a record of JOUBIN himself. He described a cranchiid found in the stomach of a *Thynnus* from the North Atlantic as *Taonius richardii* (1895, pp. 46–50). The severely damaged specimen is twice as large as *Taonidium suhmii*; its club, as illustrated by JOUBIN (Plate III, Figure 5), is exactly intermediate between *Taonidium* and *Galiteuthis*. All marginal suckers with long stalks are very small, while those of the median rows are, as JOUBIN, too, tends to assume, transformed into hooks. The characteristic form of the head, especially the eyes, resembles that of *Galiteuthis*; JOUBIN also noted the presence of a ventral pad and considers the possibility that it represents a luminous organ. The only statement which may perhaps raise doubts, is that the funnel contains a valve. However, JOUBIN himself expresses reservations on this point (p. 47), and the specimen was in bad condition. I conclude, therefore, that JOUBIN had a specimen of this genus already in 1895 which he later, in 1897, described as *Galiteuthis* from the Mediterranean. In my opinion, the differences between *Taonidium* and *Galiteuthis* are entirely due to age and are not even as great as those in the postembryonic metamorphosis of other Enoploteuthidae described by me.

The **inner organization** of the juvenile and adult specimens confirms this.

The **intestinal tract** of *Galiteuthis* is characterized by the small size of the caecum. The long stomach extends far posteriorly and consists of two sharply separated parts: the anterior part is situated behind the caecum and contains large longitudinal folds; the posterior part begins with a thickening which enters the terminal sac; two thickened longitudinal stripes extend dorsally and ventrally over the terminal sac. Its pointed, thin-walled end borders on the long gland. A ligament extends from the posterior margin to the gladius, in the normal way. At the dorsal end of the liver there are two compact pancreatic appendages; they reveal the ducts, which extend freely toward the caecum where they become united.

As regards the **genitalia**, the specimen is a very young male. A gonoduct could be found behind the branchial heart only on the left side; its apex projected freely from the small genital pocket.

I examined the **organization of** *Taonidium* in greater detail. As regards the **intestinal tract**, the relatively wide esophagus extends on the dorsal side of the liver and opens at the level of the caecum. As in *Galiteuthis*, the caecum is small and consists of a hood-shaped anterior part and a sac-shaped posterior part, both of which contain folds. To the right of the caecum there is the large gastric ganglion,
388 which I found also in the adult *Galiteuthis*. The division of the stomach into an anterior part with longitudinal folds and a smooth posterior part is not as marked as in the adult specimen. The terminal part, which is filled with flaky detritus, is sac-shaped and shows a thickened stripe only on the dorsal

side. The mid-intestine is very wide at the beginning; it contains longitudinal folds and narrows gradually to the rectum. The small appendages are large, lanceolate, resembling those of the adult.

The liver and ink sac are distinctly visible and show the normal conditions. The pancreas consists of two compact glands on the dorsal posterior side of the liver. The distinct hepato-pancreatic ducts are united close behind the heart on the ventral side of the rectum and open in the hood of the caecum as ventral canals.

Vascular system. The vena cava extends in a sinuate course on the ventral side, surrounds the right side of the liver and opens in two large venous sacs on the right side of the liver. The branchial arteries are straight and long; they originate in the ventral (anterior) venous sac and open on each side in small venous sacs which border on the branchial hearts and are about as large as these. The pallial vein forms a small but distinct venous sac which opens from the dorsal side. The gills are relatively broad, nearly oval; from them extends the branchial vein, which passes dorsally behind the branchial artery straight to the heart, without forming a swelling at its opening. The heart is spindle-shaped; the thick cephalic aorta is slightly spindle-shaped at the base and sends off the thin dorsal artery.

The **renal sacs** have distinct inner and outer openings. The inner opening, the so-called duct of the body cavity, extends obliquely anteriorly toward the outer papillae, which are situated more or less at the level of the first third of the branchial artery and are not raised like chimneys. I was unable to find the genital gland or the efferent ducts.

The inner organization of the juvenile and that of the adult form have thus distinct similarities, mainly as regards the shape of the intestinal tract and the position of the pancreas. There are certainly differences, but these are readily explained as expressions of the different stages of development.

Joubin (p. 292) came to the conclusion that the genus *Galiteuthis* should be considered as a representative of a new family, which he designates Cranchionychiae and places next to the Cranchiaeformes of Steenstrup (1861). I believe that the two groups should be united into the family Cranchiidae, because they are closely related. Joubin definitely overestimated the systematic importance of the only character which distinguishes *Galiteuthis* from the other Cranchiidae, the presence of hooks on the club. In all the other characters *Galiteuthis* resembles the other Cranchiidae so closely that I have no
389 doubt that the generic name *Taonidium* should be abandoned in favor of the older name, *Galiteuthis*, and that the entire group Cranchionychiae should be included in the Cranchiidae.

Measurements

	Station 43 (*Taonidium*)	Station 51 (*Galiteuthis*)
Dorsal length of mantle	34 mm	110 mm
Length of fins	6 mm	35 mm
Width of fin	2.5 mm	4 mm
Length of head pillar	3.5 mm	8 mm
Length of eye	3 mm	
Width of eye	2 mm	
Width of head (at eye level)	8 mm	16 mm
Length of 1st arm	2.5 mm	9 mm

Measurements (contd.)	Stn. 43 (*Taonidium*)	Stn. 51 (*Galiteuthis*)
Length of 2nd arm	4 mm	13 mm
Length of 3rd arm	5 mm	19 mm
Length of 4th arm	4 mm	21 mm
Length of tentacles	30 mm	64 mm
Length of club	5 mm	8 mm

Bathothauma CHUN

Bathothauma lyromma CHUN

(Plate LVI, Figure 9; Plate LVII, Figures 1, 2; Plate LVIII, Figures 6, 7)

Bathothauma lyromma CHUN, 1906, *Syst. d. Cranchien*, p. 86.
Bathothauma lyromma HOYLE, 1909, *Lum. org. Pacif. Ceph.*, VII. Intern. Zool. Congr. (Adv. Print).

Bathothauma is one of the most interesting Cephalopoda caught by the Antarctic Expedition. The relatively large specimen was collected on 9 October 1903 in a vertical net, at a depth of 3,000 m, in the Guinea Current west of Cape Verde. It is illustrated here with the permission of VANHÖFFEN and I shall describe it in detail elsewhere. The reader is referred to the diagnosis of the genus (p. 240) and to the data given in the general review. Another specimen of this genus was collected in the Pacific by AGASSIZ on the *Albatross*. A photograph of the specimen, sent to me by HOYLE, shows that the bend of both eye stalks was caused by an injury (Plate LVIII, Figure 6). Such a bend is absent in the Pacific specimen, so that I could draw the eye stalks in their normal condition (Figure 7).

As stated in the diagnosis of the genus (1906, p. 86), a large **luminous organ** is also present on the
390 eye of *Bathothauma*. Since the organ of the slightly injured right eye had become detached, I made sections and stained them (the specimen was fixed with sublimate). The organ was well preserved, although it formed a concavity which protruded outward, in contrast to the normal condition. HOYLE (1909) published a description of the same organ. It resembles the two luminous organs of *Desmoteuthis* (p. 283) in all essential characters.

The organ is oval, 5 mm wide and 4 mm long, and covers the ventral surface of the eyeball (Plate LVI, Figures 9, *luc.*). It shows a slight sheen of mother-of-pearl in the preserved specimen, which contrasts sharply with the dark surface of the eyeball. The posterior margin of the organ is surrounded by a stripe with a weak golden sheen. The luminous body (Plate LX, Figure 22, *phot.*) is nearly spherical in longitudinal section and consists of cells which resemble those described for *Desmoteuthis*. These cells are here slightly more densely arranged and lie along the longitudinal axis of the organ; if stained with iron hematoxylin, they do not show the characteristic black striation observed in *Desmoteuthis*. The nuclei are rounded on the bottom of the organ, more oval in the center; those situated in the periphery are densely arranged and elongate. Between the nuclei are numerous elongate fibrous cells (*str.*) which extend radially toward the surface and form a kind of lens; they are slightly thinner here but resemble in their structure those found in *Desmoteuthis*. HOYLE thinks that the luminous cells become more elongate and gradually pass into the fibrous cells; it should however be stressed that these are in fact two histologically distinct elements, which differ sharply from each other even where they are in contact (see Figure 19).

The reflector (*refl.*) is a cup the base of which forms a thick pad around the luminous body. It ends truncate on the outside without tapering, but flattens and extends along the eyeball on the inner side. The reflector consists of dense cells of connective tissue with oval nuclei. These cells pass gradually into fibers toward the periphery on the longer anterior margin. The spindle-shaped cells resemble the squamous cells described above, but are loosely arranged and contain small, strongly refractile granules.

Behind the reflector there is a pad of connective tissue without pigment. Here extend larger vessels (*ven.*) the branches of which pass straight through the reflector and form a capillary network inside the luminous body. The nuclei of the vessels are oblong-oval; they indicate the direction of the vessels inside the luminou body.

Fine nerves also penetrate inside the luminous body, Their fibrils stain black with iron hematoxylin and can be followed in the reflector and also in the luminous body.

The posterior surface of the organ is covered by a thick layer of fibers with nuclei (*fibr.*) which extends from the outer margin of the reflector along the loose pad of connective tissue. This layer also
391 stains black with iron hematoxylin. It is apparently this fibrillar connective tissue that causes the golden sheen at the posterior margin of the organ.

The outer skin forms a thin layer over the organ and closely adheres to it in the area of the fine systems of fibers which form the lens.

The capillary network and the nerve supply of the luminous body were not mentioned by Hoyle. I found no indication of a second organ inserted in the large sickle-shaped organ, as in *Desmoteuthis.*

Stalk-Eyed Larvae of Cranchiidae

(Plate LXI)

In addition to the larvae of *Cranchia* and *Liocranchia* mentioned above, the expedition collected some of the remarkable stalk-eyed larvae which had been collected by the *Challenger* Expedition and were drawn by Willemoes-Suhm, who considered them erroneously as gymnosomatous Pteropoda. They were described by Ray-Lankester (1884, *Quart. Journ. Micr. Sc.*, Vol. XXIV, pp. 311–318, Figures 1, 2) as *Procalistes suhmii* and stressed their relationship with *Cranchia.* Hoyle (1886, *Rep. "Challenger" Ceph.*, pp. 195–198) discussed their relationships in detail and concluded that they belong to the genus *Taonius.* His illustrations (Plate XXXII, Figures 10, 11) are much more correct than those published by Willemoes-Suhm or Ray-Lankester, as regards their outer form. The species name *T. suhmii* was transferred by Hoyle to an older specimen, for which later Pfeffer (1900) created the new genus *Taonidium.* I have shown above (p. 301) that *Taonidium* is a juvenile form of *Galiteuthis.*

The larvae described below differ markedly from *Procalistes suhmii*; they are suitable objects for those inclined to establish new genera and species on the basis of relative or juvenile characters. I shall attempt to prove, at least as far as this is possible for older larvae, their connection with adult stalk-eyed Cranchiidae.

1. Large larva from Station 64, near S. Thomé, 0°25′ N, 7°0′ E. Vertical net to 2,000 m (Figures 9, 10)

The larva has a dorsal mantle length of 9 mm and is 11 mm long without the tentacles, which are 9 mm long.

The mantle has the shape of a deep goblet, is only slightly constricted at the margin, and has a pointed posterior end. The small fins are nearly semicircular and do not project beyond the mantle. The funnel is large and extends almost to the base of the tentacles.

392 The head forms a short, thick head pillar which bears the large buccal cone. The eye stalks are short, plump and slightly swollen by the large optic ganglia. The large, oval eyes show a ventral thickening but no distinct process. The thick optic nerve and the two ophthalmic nerves are visible through the stalks.

The arms are still very retarded. The 1st and 2nd arms are larger, the 3rd arms are smaller and the 4th arms are short. All arms bear suckers. There are 4 pairs of suckers on the 1st and 2nd arms, 3 pairs on the 3rd arms, and 2 on the 4th arms. The tentacles are very large (Figure 10) compared to the small arms. They are distinctly divided into a stalk and a club. Biserial alternating pairs of stalked suckers are situated on the stalk almost to the base. Only towards the club is an indistinct arrangement in 4 rows of suckers recognizable; it passes into the proper arrangement in 4 rows of slightly larger suckers on the club. Neither the suckers on the arms nor those on the club show any dentition. Protective membranes are present on the club, but a keel (swimming membrane) is absent.

The coloration of this transparent larva is caused by large reddish brown chromatophores. These are irregularly scattered on the mantle, but the 2 posterior chromatophores are situated symmetrically on the base of the fins. Large chromatophores are also present on the head, especially on the eye stalks and eyes. There is also a row of chromatophores along the outer side of the tentacles.

Should one attempt to relate our larva back to an aberrant, stalk-eyed member of Cranchiidae, then one would find its characteristic form to agree most closely to that of *Taonidium*. Other possibilities are *Corynomma* and *Teuthowenia*. However, *Corynomma* can be excluded because the eye stalks are plumper and the suckers on the stalks form 2 rows and not 4, as in the juvenile *Corynomma*, and *Teuthowenia* can be excluded because of the slender body and the pointed posterior end of our larva.

The **inner organization** also resembles that of *Taonidium*, particularly the form of the intestinal tract. The esophagus opens in a large sinus situated far behind the liver at the level of the small caecum, which is situated on the left side. The sinus narrows only slightly, where it opens into the sac-shaped stomach which tapers posteriorly and reaches almost to the posterior end of the body. Here the stomach is attached by a short gastro-genital ligament to the dorsal side close to the spoon-shaped widening of the gladius. While the end of the gladius does, in fact, resemble that in *Cranchia*, it is nevertheless more pointed. From the sinus there extends also the short intestine which surrounds the posterior side of the ovoid liver and receives the efferent duct of the ink sac as usual. Left and right of the liver, and closely adhering to it, are the two pancreatic glands from which ducts without pancreatic lobes
393 extend to the caecum.

Only *Taonidium*, *Corynomma* and *Teuthowenia* show similar conditions. However, the caecum of *Corynomma* adheres to the lower side of the liver, and *Teuthowenia* does not have that elongated, joint gastric sinus.

The vascular system gives no definite information on the relationships; however, the branchial arteries are long and form a small venous sac before opening into the branchial heart.

I conclude, therefore, with a fair degree of probability that the large larva belongs to the developmental cycle of *Taonidium* (*Galiteuthis*).

2. Larva from Station 143, Antarctic Drift Current, 56°43′ S, 32°6′ E. Locking net, 200–100 m (Figure 6)

The larva has a dorsal mantle length of 5.5 mm and is 7 mm long, excluding the curved tentacles which are about 2.5 mm long.

The mantle is slender goblet-shaped, with a pointed posterior end and small spatulate fins which are situated on the posterior lateral margin of the gladius; the latter widens only gradually.

The funnel does not project far and leaves most of the head free. The head ends in a short pillar which bears the buccal cone. The eyes are slightly oval; the eye stalks are broad, but narrower than in the larva described above.

The arms are so underdeveloped that I have hardly ever observed their like in larvae of Enoploteuthidae of the same size. The 1st and 2nd arms are short stumps with 3 to 4 suckers; the 3rd arms are hardly visible as minute tubercles, and there is no trace of the 4th arms. The tentacles, too, are relatively small, curved posteriorly and completely covered with suckers that are arranged in 4 rows from the base. A differentiation into stalk and club is not recognizable.

The larva is covered with contracted rust-red chromatophores which have no recognizable symmetrical arrangement, at least not on the mantle. Isolated chromatophores are present on the head and eyes and, in a uniserial arrangement, on the outer side of the tentacles.

The systematic position of this larva is determined mainly by the tentacles. In older and younger larvae of other stalk-eyed Cranchiidae the division of the tentacle into stalk and club is made possible by the arrangement of the suckers in 2 rows on the stalk, and 4 on the club. Only the genus *Corynomma* shows in younger specimens an arrangement of suckers in 4 rows on the stalk. Moreover, I feel justified to place this larva with *Corynomma*, the more so as its **inner organization**, too, resembles that of the
394 adults: The pancreatic glands are situated on both sides close to the posterior surface of the liver; the efferent ducts surround the mid-intestine and are united immediately behind it before opening in the small caecum, the latter is situated not far from the liver on the common gastric sinus, which passes into the stomach without a constriction; the stomach extends only to the posterior third of the mantle. This condition is definitely in agreement with that of the intestinal tract of *Corynomma*.

The inner organs of the larva are well preserved. The posterior salivary gland is visible dorsally, at the level of the large static organ. Behind the gland are the stellate ganglia, which are situated close together. Behind the apex of the stomach there is a broad, heart-shaped "anlage" which is probably an early developing genital gland.

As regards the vascular system, the vena cava is very distinct; it surrounds the right side of the liver and branches into two large branchial arteries which are slightly curved anteriorly and form small venous sacs anterior to the branchial hearts; the gills are very small; from them extend two long branchial veins which show no dilatation and extend dorsally from the branchial arteries to the heart; the latter is situated between the right pancreatic gland and the gastric sinus.

I conclude, therefore, that the larva belongs to *Corynomma*.

3. Larva from Station 135, Antarctic Drift Current, 56°30′ S, 14°29′ E. Vertical net to 1,500 m (Figures 7, 8)

The larva has a dorsal mantle length of 3 mm and its total length is 5 mm, excluding the relatively long tentacles: 5 mm.

The mantle is sack-shaped and rounded posteriorly; the fins are small and spatulate; the funnel is large and extends to the base of the tentacles; the head is broad and ends in a short pillar which bears the buccal cone.

Compared with the older larvae described above, the arms are not as small as could be expected in view of the small size of the larva. The 1st and 2nd arms are distinctly recognizable and bear two pairs of suckers; the 3rd and 4th arms form small stumps. The tentacles (Figure 8) are very large, almost as long as the body. They bear stalked suckers almost to the base and are divided, if only indistinctly, into a stalk and a club. The stalk bears suckers arranged in 2 rows which gradually pass into one row toward the club. The club has no membranes.

The oval eyes are moderately large and have broad, plump stalks which are almost entirely occupied by the large optic ganglia.

This larva is also covered with rust-red chromatophores on the mantle, funnel, base of the head and outer side of the tentacles.

The shrinking of the mantle obscured the inner organs, but it was recognizable that two large pancreatic glands are situated on the sides of the liver, as in *Teuthowenia.* This larva apparently be-
395 longs to *Teuthowenia antarctica.* The plump, sac-shaped body, the tiny fins, the thick eye stalks and their large optic ganglia, the arrangement of the suckers on the tentacles—all these characters resemble the juvenile *Teuthowenia* so closely that other Cranchiidae seem to be excluded. Moreover, the larva was collected in the same area in which we caught a specimen of *Teuthowenia antarctica*: at the edge of the antarctic ice.

4. Youngest larvae (Figures 1–5)

The youngest larvae can, of course, not be identified with certainty. The first specimen I shall describe is a plump, sac-shaped larva, 3.2 mm long (Figures 1, 2). This larva was caught at Station 102 in the warm waters of the Agulhas Current; the tentacles, and apparently also the ends of the larger arms, were lost.

This larva has a sac-shaped, posteriorly rounded mantle with very small fins, a small funnel and a slender head cone on which the "anlagen" of the 3rd and 4th arms are recognizable. The huge, oval eyes are situated on the optic ganglia, which are displaced toward the head pillar. Each eye bears a distinct, ventrally produced fovea; their distinctness is the reason why I describe this larva first. Since I have so far not studied the eyes of Cranchiidae in detail, I do not know whether such a fovea is present in the stalk-eyed forms. If this is the case, it may furnish an indication on the systematic position of the larva. The inner organs are too larval to provide any clue: the gills have only 4 lamellae; the slender ink sac is situated on the nearly spherical liver; the caecum, the tubular pancreatic appendages and the short stomach are situated close together.

The younger stalk-eyed cranchiid larva (Figures 3–5) was caught with a vertical net at Station 41 (Guinea Current). It is 2.8 mm long and slender. The goblet-shaped mantle has a slightly pointed posterior end, with very small fins. The funnel extends far anteriorly to the buccal cone and covers the slender head pillar. The eye stalks and the relatively small eyes are also more slender than those in the forms described above. The head pillar bears very small 1st and 2nd arms and small tentacles. There is no trace of the 3rd and 4th arms. The stump-shaped 1st arms bear one sucker; there are 2 suckers on the 2nd arms, and 6 on the tentacles.

If it be permissible at all to attempt a determination of such a young larva, the small eyes and the relative length of the eye stalks suggest *Euzygaena.*

396 Older larvae of stalk-eyed Cranchiidae can be determined to their genus and species with any degree of certainty only by taking their entire organization into account. The external characters undergo so great a change in the course of postembryonic development that the inner organization, especially the intestinal tract and its glands, have to be examined to determine their systematic position. The important systematic characters—of the Cranchiidae in particular and of the Oegopsida in general—develop only during postembryonic development. The dentition of the suckers and their reduction or transformation into hooks; the form of the cone of the gladius; the form and relative size of the fins; the presence of membranes on the arms and on the tentacle club; the relative size of the arms, eyes, head and funnel; the gradual development of luminous organs and olfactory tubercles—all these may attain their definitive form at an early or a very late stage.

The study of the postembryonic development of the Oegopsida is exceedingly fascinating, but poses difficult problems for the unprejudiced observer. If henceforward greater care will be taken in the evaluation of relative and larval characters for the establishment of new genera and species, then the labor involved in the clarification of the postembryonic development of some Oegopsida and the elaboration of a system based on their inner organization will have been worthwile.

Carl Chun

THE CEPHALOPODA

PART II: MYOPSIDA, OCTOPODA

TEXT

GERMAN DEEPSEA EXPEDITION 1898–1899. VOL. XVIII, PART II

WISSENSCHAFTLICHE ERGEBNISSE

DER

DEUTSCHEN TIEFSEE-EXPEDITION

AUF DEM DAMPFER „VALDIVIA“ 1898-1899

IM AUFTRAGE DES REICHSAMTES DES INNERN

HERAUSGEGEBEN VON

CARL CHUN

PROFESSOR DER ZOOLOGIE IN LEIPZIG, LEITER DER EXPEDITION

UND NACH SEINEM TODE FORTGESETZT VON

AUGUST BRAUER

PROFESSOR DER ZOOLOGIE IN BERLIN

ACHTZEHNTER BAND

CARL CHUN

DIE CEPHALOPODEN

II. TEIL:

MYOPSIDA. OCTOPODA

MIT 39 ABBILDUNGEN IM TEXT UND 34 TAFELN

JENA

VERLAG VON GUSTAV FISCHER

1915

Eingegangen im März 1914, C. Chun

Myopsida D'ORBIGNY, 1839

Family **Sepiolidae** LEACH, 1817

Rossia OWEN, 1834

Rossia mastigophora CHUN

(Plate LXII, Figures 1–3; Plate LXIII, Figures 1–6)

Locality: Station 253, Indian North Equatorial Current, 0°27′ S, 42°47′ E. Trawl, 638 m. Three specimens (two females, one male).

At Station 253 near the East African coast, trawling at a depth of 630 m, we collected 3 specimens of a new species of the genus *Rossia*. The largest specimen was a mature female, the smaller ones were a male and a younger female. As the animals were alive, we made color sketches which showed the striking sky-blue tone of the interior of the eye. This new species shows a number of interesting characters and will be compared with the known species of *Rossia*. This is a deepwater form the eyes of which are as large as those of other species of *Rossia* from greater depths.

The **mantle** is sac-shaped and rounded posteriorly; there are no tubercles or papillae, in contrast to *R. glaucopis* LOV. Its margin was slightly retracted, especially on the dorsal side, and there were no projecting corners. This is important because VERRILL (1881, p. 349, Plate XXXVIII, Figure 1) described a dorsally projecting mantle corner as a specific character of the related species *R. megaptera*.

The **fins** are relatively large, longer than wide, and occupy at least two-thirds of the length of the mantle; their base is situated close to the anterior mantle margin. The funnel is slender; its circular or oval opening projects to the level of the middle of the eye and the small funnel valve is visible inside it. A distinct funnel valve is absent.

The funnel cartilages are 13 mm long and have a deep groove which widens slightly anteriorly and gradually flattens posteriorly (Plate LXIII, Figures 4, 6). The margin of the cartilage is folded over
406 like a collar and is moderately broad; in the larger female it was situated close to the surface, in the male it projected from the surface. The opposite cartilage of the mantle, which fits into the funnel groove, is slightly longer than the funnel cartilage; it forms a ridge which extends almost to half of the level of the gills (Figures 4, 5). The outer adductors extend toward the anterior margin of the

funnel cartilages; they are inserted at the ventral posterior margin of the eyes and become more distinctly visible only near the funnel cartilage.

The **funnel organ** (Figure 5, *org. inf.*) is very large, particularly the single, median dorsal part, which is divided before the anus into two broad lobes that extend posteriorly to the accessory nidamental glands at the level of the middle of the gills.

The **collaris** extends broadly to its insertion on the **neck cartilage** (Plate LXIII, Figure 3). The mantle margin was slightly recurved so that the cartilage was visible as an oval formation of 12 mm length and 4 mm width. Posteriorly the cartilage is slightly narrower, due to the insertion of the collaris; its narrow, whitish margin encloses a depression for the narrow opposite cartilage of the mantle. The structure of the mantle cartilage provides clear-cut proof of the specimens' belonging to *Rossia*: the closing apparatus of the neck is completely developed and not fused with the mantle margin. This is the most important difference between *Rossia* and *Heteroteuthis* in which a partial fusion is already present, as shown by Appellöf (1898, p. 578, Text Figure 2).

The slightly constricted neck region has no folds; it passes into the large head which is at least as wide as the mantle margin. The large size of the head is caused by the large **eyes** the length axis of which measures 23 mm in the adult female, of which the lens takes up 19 mm. The dorsal margin of the iris projects in a shallow curve and slightly narrows the pupil through which the sky-blue fundus of the eye is visible in life. The lid fold projects markedly at the ventral margin.

The **olfactory organ** (Plate LXIII, Figure 4, *olf.*) was in all specimens difficult to find. It is situated on the lateral posterior surface of the eye, 4 mm behind the lid margin, and forms a wall which is 1.5 mm wide and encloses a pit.

The **arms** are moderately large and there are no marked differences in length between them. The formula is 3, 4, 2, 1 in both the female and male.

Protective membranes are hardly recognizable. There are, however, processes at the outside of the conical base of the stalk of each sucker, on the proximal part of the stalk. These processes may be considered as traces of the muscular bridges of the protective membranes. Swimming membranes are distinct on the 3rd arms but they are hardly recognizable on the 1st and 2nd arms. Outer membranes are almost absent between the ventral arms but between the 3rd and 4th arms they are well developed and extend far along the arm, reaching the tips of the 4th arms on the dorsal margin. Between the 1st, 2nd, and 3rd arms the outer membranes are only weakly developed, their size decreasing toward the base from the 3rd to the 1st arms.

407 The **arm suckers** are biserial in all specimens. This species therefore belongs to *Franklinia*, a subgenus of *Rossia* established by Joubin (1902) and characterized by the biserial arrangement of the suckers. They are situated on conical pads, alternate as usual and are easily lost in preserved specimens. Their opening is narrowed and has a smooth margin.

The **tentacles** are relatively long and have an unusually large club, 34–38 mm long, which forms a third of the length of the stalk. The stalk has a flat inner side; its outer side is bordered by edges, especially in the distal part. A shallow, gray groove is present on the inner side.

The **club** (Plate LXIII, Figure 2) is dorsally curved like a horn, on the right tentacle of the large female it was curved into a spiral. A protective membrane is present at the dorsal proximal end of the club, but it is weakly developed and barely indicated on the ventral side. The keel is distinct and dorsally displaced and apparently causes the more or less marked spiral coiling of the club.

The proximal part of the sucker-bearing surface of the club is not widened into a disc but is slender. The club widens distally and surrounds two-thirds of the tentacle stalk.

The suckers of the tentacles are so small that they are hardly visible with the naked eye. They are

only 0.15–0.17 mm wide, so that they are among the smallest suckers of the tentacles in the Decapoda. Their umbrella-shaped margin is finely striated, and their inner side shows the usual polyhedral pattern in 4 rows. The chitinous ring is smooth, without denticles; it continues in a relatively thick chitinous cup which is open at the bottom. Particularly characteristic for this species is the large number of suckers, which form oblique rows. It is difficult to count them, but there are at least 30–40 in each such row. The stalks of the suckers are deeply embedded in the tissue, so that a shallow incision of the sucker-bearing surface shows their bases, which cross each other diagonally. Seen from the outside, these rows are less distinct.

The above-described form of the club is an important character of this species. In surface forms, e.g. in *R. macrosoma*, the club forms a disc-shaped proximal widening, caused by the ventral protective membrane which bears almost half of the suckers. A dorsal protective membrane is present but it is small and passes into the ventral membrane on the disc-shaped base of the club. The swimming membrane (keel) is also displaced to the dorsal side and its strong development causes the dorsal outer curving of the club. In the proximal part, the dorsal suckers are larger than the ventral ones and form transverse rows of 10–12.

This structural feature of the club is present in almost all species; *R. mölleri* STEENSTR. has particularly large suckers on the club. In forms living at greater depths, e.g. *R. megaptera* VERR. and *R. caroli* JOUB., the disc-shaped widening of the club is less distinct and the suckers of the tentacles are
408 small. However, the sucker-bearing surface of the club of these species is narrow and the suckers in the transverse rows are less numerous than in *R. mastigophora*. At any rate, the form of the club is one of the important specific characters of this species.

The **buccal funnel** is low and has 6 peaks. They are supported by buccal pillars (supports) from the base of which extend the buccal attachments to the arms. The 1st and 2nd arms are attached dorsally, the 3rd and 4th arms ventrally. The swollen, distinctly fluted inner lip protrudes from the buccal funnel; the outer lip forms only a narrow seam at the base of the inner lip. The lare longitudinal muscular cords are distinct on the ventral arms which converge toward the base of the funnel in the preserved specimen.

Hectocotylization. Already from the outside one could distinguish the small male from the two females by the form of the suckers on the arms. This specimen was, however, not yet fully mature and the transformation of the two dorsal arms which is typical for *Rossia* had not yet taken place. But that it was indeed a male was proved by the enlargement of some suckers of the arms, which attain a diameter of 2.5 mm. There are about 8 pairs of enlarged suckers on the ventral arms, beginning from the second proximal pair. A similar condition is present also on the 3rd arms, while the 2nd arms bear about 6 pairs of enlarged suckers. The suckers of the dorsal arms are not so markedly enlarged but some of them are irregularly arranged.

The **coloration** of the 3 specimens was rather vivid. The dorsal side, head and fins had the yellowish brown color of burnt sienna. This coloration, which is caused by chromatophores, is weaker on the outer side of the arms and on the ventral side of the body. The dark eyeball peculiarly contrasts with the sky-blue interior of the eye; this is a specific character of this species. Though cases of a purple-red color of the interior of the eye of live Cephalopoda are occasionally found in the literature (cf. *Calliteuthis*, Plate XVIII, *Benthoteuthis*, Plate XXVI, *Doratopsis exophthalmica*, Plate XLVI, *Bolitaena diaphana*, Plate LXXXIII, Figure 1), this "real eye-blue" is specific for *Rossia mastigophora*.

Mantle complex

(Plate LXIII, Figures 4, 5, 6)

Opening of the mantle cavity from the ventral side after cutting through the musculus adductor pallii medianus shows that the two arms of this muscle circumscribe the rectum all the way except for a small part. Near the anus lie the two spatulate anal appendages which are symmetrically halved. The funnel depressors (*depr. inf.*) are slender and extend broadly from the mantle, behind the base of the gills. This constitutes a distinct difference from the forms which have a completely closed muscular
409 capsule around the liver and in which the funnel depressors are situated on the liver capsule and do not reach the mantle. When discussing another family, we shall see that this condition applies also to *Spirula*. The vena cava passes on the right side near the adductor pallii medianus.

The testis (Figure 4) is only indistinctly visible through the posterior part of the abdominal wall. The windings of the spermatophore gland are visible behind the left branchial heart and fill the space to the middle of the mantle adductor. The cylindrical, tapering penis (*pen.*) projects far into the anterior part of the mantle cavity on the left side. Near its base one sees the chimney-like processes of the papilla of the left renal sac; the right papilla (*ur.*) is displaced slightly posteriorly.

The renal papillae of the female (Figures 5, 6) are less distinct. If the visceral sac is pressed aside, one detects the left papilla which is situated between the terminal part of the oviduct and the accessory nidamental gland; the opening of the oviduct projects far beyond the papilla. The two papillae are situated at the same level and are covered ventrally by the large nidamental glands (*nid.*). They are pear-shaped, posteriorly joined in the middle, anteriorly tapering, and are 15 mm long. Anteriorly and dorsally to the nidamental glands lie the accessory nidamental glands (Figure 6, *nid. acc.*) which are 7 mm long and have a wide opening at the level of the tip of the proper nidamental glands.

The **oviduct** and its surroundings are of particular interest, since they show distinct differences from the condition known so far in *Rossia*. There is no trace of a pocket for the reception of spermatophores from the bottom of which projects the opening of the oviduct. In contrast to *Rossia macrosoma*, which was examined in detail by Rakowitza and Döring, the oviduct of the younger and the older female is completely free and is attached only dorsally to a ligament which lies in the left part of the mantle cavity. The oviduct begins broadly behind the base of the left gill, then tapers anteriorly and opens in a narrow slit which is 3 mm long. The free terminal part of the oviduct, which projects with its opening beyond the left arm of the funnel organ, is 13 mm long. The oviduct gland is only weakly developed; its ring system at the base of the slit-shaped opening is well differentiated from the fork system, which extends to the tip. The maturity of our specimen is, however, proved by the large ovary; the ripe eggs are 3 mm large and are visible through the abdominal wall.

Finally, I should like to note certain peculiar structures in the mantle cavity—two pairs in the male and one pair in the female. They form rounded or oval, lens-shaped elevations situated on the left and right side of the rectum, behind the renal papillae, close to the middle of the adductor pallii medianus (Figure 4, *gl.'*, *gl.''*). Such structures are so far unknown in the genus *Rossia* and I made sections of the anterior and the posterior pads of the male. They were found to be lens-shaped glands situated on a stroma of loose connective tissue with capillaries. Numerous, dense gland tubercles
410 extend from the surface to near the center of the pad. These tubules consist of cuboid or short, cylindrical gland cells with spherical nuclei; they open at the surface almost unconstricted. The epithelium between the tubules shows supporting cells and its drawn-out oval, strongly staining nuclei differ sharply from the spherical, pale nuclei of the gland. The finely granulate layer which covers the entire surface of the gland seems not to have been formed by the secretion but to comprise a layer of cilia.

I do not know the function of these glands. Luminous organs are present in various Sepiolidae, as shown by Meyer for *Sepiola* (1906) and *Heteroteuthis* (1908), and by Wülker (1910) for *Euprymna* and *Inioteuthis*. These luminous organs are large glandular complexes situated in pairs on the ink sac and equipped with a reflector. Lo Bianco observed that they produce a luminous secretion.

In this case, there are much simpler and smaller formations, which show no relation to the ink sac and have no trace of a reflector. I hesitate to interpret them as luminous organs because of the absence of a reflector.

I rather would consider these glands to be homologous with organs which Wülker (1912) recently found in males of *Loligo forbesi* and interpreted as rudimentary accessory nidamental glands. They are paired and are situated on the ventral side of the ink sac, in front of the renal papillae, and their fine structure closely resembles that of the organs in *Rossia*. In contrast to similar organs found by Naef in the male of *Sepietta minor*, the tubules of these organs degenerate with age.

As to Wülker's interpretation of these organs as rudimentary accessory nidamental glands, it could apply in *Rossia* only to the posterior pair of glands of the male, but not to the anterior pair, which is present in both sexes and is situated behind the anus outside the area of the genital openings.

The posterior pair of glands is present only in the male. Both in the large, mature female and in the smaller one I failed to detect such glands behind the renal papilla near the adductor pallii medianus, although I examined them carefully. In them the place of the glands is occupied indeed by the accessory nidamental glands, which form flat oval discs in the younger female.

If Wülker's interpretation is accepted for the posterior pair of glands it should be considered that the anterior and posterior glands show exactly the same structure. Their structure resembles Wülker's description so closely that I did not find it necessary to illustrate them.

There is thus a different morphological interpretation for two pairs of glands of the same structure: the anterior pair can definitely not be considered as rudimentary accessory nidamental glands, but the posterior pair may well be regarded as such.

411 Since we have no information on the function of these glands (according to Wülker, they do not emit light in the live animal) or on their occurrence among the Myopsida, further studies are necessary.

Measurements

	Large female	Male
Length of mantle (dorsal)	46 mm	31 mm
Width of mantle (margin)	37 mm	26 mm
Base of fins	29 mm	16 mm
Length of fins	33 mm	
Width of fins	22 mm	17 mm
Neck cartilage, length	12 mm	7.5 mm
Neck cartilage, width (anterior)	4 mm	
Funnel cartilage, length	13 mm	8 mm
Funnel cartilage, width (anterior)	5 mm	
Mantle cartilage, length	15 mm	
Width of head	37 mm	25 mm
Thickness of eye (dorsoventral)	21 mm	
Width of eye	23 mm	17 mm
Diameter of lens	19 mm	

Measurements (contd.)	Large female	Male
Length of 1st arms	36–37 mm	25 mm (left) 29 mm (right)
Length of 2nd arms	39–40 mm	23 mm
Length of 3rd arms	44 mm	30 mm
Length of 4th arms	39 mm	29 mm
Stalk of tentacle (without club)	67 mm	
Right club	38 mm	
Left club	34 mm	

Family **Sepiidae** D'ORBIGNY, 1845

Sepiarii STEENSTRUP, 1861

Hemisepius STEENSTR., 1875

Hemisepius typicus STEENSTR.

Hemisepius typicus STEENSTRUP, "*Hemisepius*", *Vidensk. Selsk. Skr.*, 5. R. nat. math., Part 10, Vol. VII, Copenhagen, 1875, pp. 465–479: Plate I, Figures 1–10; Plate II, Figure 1.

Locality: Station 100, Francis Bay, shallow water in northern part of Agulhas Bank. Blake Dredge. 34°9′ S, 24°59′ E.

412 The rediscovery of *Hemisepius typicus* STEENSTR. was of particular interest. We found two specimens in the shallow water of Francis Bay, southern Cape Province, close to the area (Simons Bay) where the specimens described by STEENSTRUP were collected. This seems to indicate that the genus has a restricted distribution. Since the larger specimen turned out to be a male, and males were not known until now, I am now able to complement STEENSTRUP's description. The specimen was slightly damaged by the dredge but shows distinctly the typical characters of *Hemisepius* (Text Figure 33). The smaller specimen was a female and I gave it to my student STICH for a study of the characteristic shell.

The **male** is 34 mm long to the tip of the 4th arm; the mantle is 17 mm long. The maximal width is 14 mm and the head is 12 mm wide. This is obviously a species which becomes mature while still small of size. It shows a typical character of *Hemisepius*: the two longitudinal ventral strips of glands. According to STEENSTRUP, his specimens have 12 nipple-shaped glandular pads on each side. There were 15 glands on the right side and 12 glands on the left, with distinct openings. Sections through the glands of the small female show that they are deeply embedded in the cutis and consist of elongate cells. The cells are arranged in lamellae which have drawn-out oval nuclei and project far into the lumen of the gland. Almost round nuclei are present only at the base of the gland.

STEENSTRUP thinks that this arrangement of the glands is characteristic for *Hemisepius*, in distinction to *Sepiola*. This seems doubtful because some species of *Sepiola*, too, have in the identical sites longitudinal ridges, apparently formed by confluent mantle glands; but this needs further study.

413 The arm apparatus of the male differs in some characters, in addition to the hectocotylization, from STEENSTRUP's description. The protective membranes are moderately developed, and the outer membranes form a distinct umbrella which was not mentioned by STEENSTRUP. The suckers are biserial, almost spherical, and not so strongly flattened as in the female. They show the following peculiarity.

The rows of paired suckers on the dorsal arms begin with one large proximal sucker, followed by 11 pairs, of which the 10th is slightly larger; then follow 3 smaller pairs and at the tip, very small suckers. The 2nd arm shows a similar condition. The 3rd arm shows no marked enlargement of any pair of suckers. The right ventral arm bears 13 pairs of suckers which distally gradually decrease in size.

FIGURE 33. *Hemisepius typicus* STEENSTR.
Male with hectocotylized left ventral arm; ventral view.

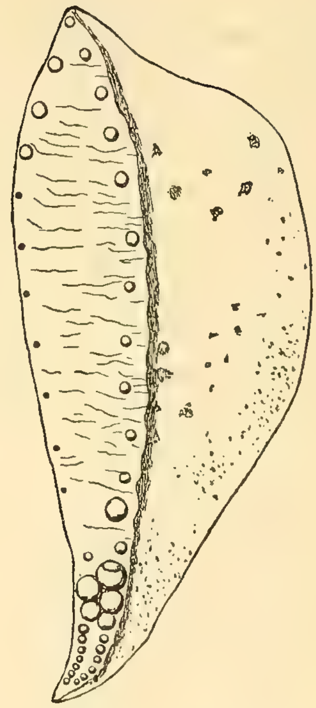

FIGURE 34. *Hemisepius typicus.*
Hectocotylus (left ventral arm).

The left ventral arm is transformed into a **hectocotylus.** Its inner side is widened and bears weak transverse wrinkles. Toward the outer side it sharpens into a keel. The suckers of this arm show a characteristic arrangement: proximally they are widely spaced and some of them are almost completely reduced; only in the short distal part they show the normal arrangement. Both rows (Text Figure 34) begin with one small proximal sucker, followed on the dorsal margin by 10 small suckers, then a large 11th, and finally a 12th sucker. Some of the suckers on the ventral margin are strongly reduced; this margin has at first 3 proximal suckers, then 8 tiny, rudimentary suckers which are hardly recognizable; distally, at the tip, an abrupt increase in size takes place; they comprise here 5 suckers in 2 rows, followed on the ventral margin by 7 and on the dorsal margin by 6 small suckers which gradually decrease in size toward the tip.

Family **Spirulidae** OWEN, 1836

Spirula LAMARCK, 1799

Spirula australis LAMARCK
(Plates LXIV–LXIII)

Locality: Station 195: Nias South Canal, 20 nautical miles south of P. Nias. 0°30′ N, 98°14′ E. Trawl, 594 m (the trawl did not touch the bottom).

The expedition caught a specimen of *Spirula* at Station 195 in the Nias South Canal. The animal was caught by a trawl that descended the steep continental slope to a depth of 594 m without touching
414 the bottom. It must therefore belong to the pelagic animals, as is also evidenced by the fact that the trawl contained other organisms that usually are caught only with vertical nets. The specimen was in good condition, although the layer of chromatophores on the mantle was chafed off by the net. Only at the posterior end, the fins, head and arms the layer remained intact. Our hope of collecting a second specimen of this rare organism was not fulfilled and we had to be grateful that—like the *Challenger* and *Blake* Expeditions—we, too, had now attained possession of this valuable form. The specimen was preserved in formol and transferred to alcohol on the next day. The preservation of the soft parts and tissues was satisfactory.

1. History

Since only a few specimens of *Spirula* have been collected until now, it is in order to provide a review of the literature and a discussion of the validity of the species described.

Spirula was discovered by PÉRON during his voyage around the world in 1800–1804. PÉRON illustrated it in the first edition of his report of the voyage, published in 1807 and 1810, with 37 plates. I have only the 2nd edition of this work (1824), edited by FREYCINET after PÉRON's death, which contains the plate under reference, too.

PÉRON, Franc.: *Voyage de découvertes aux terres Australes fait par ordre du governement sur les corvettes le Géographe, le Naturaliste, et la goilette le Casuarina pendant les années 1800, 1801, 1802, 1803 et 1804.* Historique, rédigé par PÉRON et continué par M. LOUIS DE FREYCINET. Vol. 4. Atlas de 68 planches par Lesueur et Petit. II. edit. par L. DE FREYCINET, Paris, 1824.

PÉRON's illustration bears the caption *Spirulea prototypos.* It has been copied repeatedly and included in many publications, although it is readily seen that the posterior end of the body was torn off. It shows a brightly purple color of head and arms, and the shell is exposed posteriorly. The catch is not mentioned in the text. According to BLAINVILLE (*Dictionnaire des Sciences Naturelles*, Vol. 50, 1827, p. 305), the specimen was found adrift in the open sea between the Moluccas and Isle de France.

ROISSY (1805, pp. 9–15) published the first details on PÉRON's specimen and placed it in the Cephalopoda.

Denys-Montefort: *Histoire Naturelle générale et particulière des Mollusques*; suite aux oeuvres de Buffon. Paris an XIII, 1805. Vol. V par Félix de Roissy.

Roissy mentions that it has 8 arms, two tentacles, sessile eyes and an internal shell.

This is also the opinion of Lamarck, who described it as *Spirula australis* in the *Encyclopédie*
415 *méthodique*, Plate 465, Figure 5 a, b. I was unable to obtain the respective volume of the *Encyclopédie* and ascertain the year in which the name "*australis*" was given. However, this volume was apparently published before Péron's report, because later French authors give "*australis*" priority over "*prototypos*" without indicating the year.* The illustration of Lamarck, which was copied by later authors, e.g. Gray (1845), differs markedly from that of Péron. Lamarck's illustration appears to have been only a rough sketch, perhaps drawn up for a lecture, so that the arms (shown correctly by Péron) are drawn too long.

The first detailed description of the specimen caught by Péron was presented by Lamarck in the first edition of the *Histoire naturelle des Vers*. He does not retain the name "*Sp. australis*" but changes it to "*Sp. peronii*", in honor of the discoverer.

The specimen has disappeared from the Paris Collection and has not been found since. What is important for the nomenclature is that it was given no less than three names:

Sp. australis Lamarck,
Sp. péronii Lamarck, 1815–22,
Spirulea prototypos Péron, 1807.

Further catches of *Spirula* were recorded only thirty years later, namely on 12 January 1836, when the corvette *La Recherche*, commanded by Captain Tréhouart, collected several specimens between the Canaries and Cape Blanco (24°28′ N, 20°22′ W), at the surface. Robert reported on these specimens in a letter to Blainville, published in the *Comptes rendus* (Vol. II, 1836, pp. 322, 362). The specimens were badly mutilated and had apparently surfaced from great depths and then fallen prey to Physaliae. Nevertheless, Robert was able to demonstrate the two small fins, and the peculiar posterior end which forms a "bouton terminal", as he calls it. In one specimen, one eye was still present in a cartilaginous cavity, and a funnel in another specimen. The coloration, described to resemble white coffee, is explicitly attributed to the brown chromatophores.

M. H. de Blainville presented a more correct description of these specimens in the *Annales Francaises* (Vol. I, 1837, pp. 368–382). The figures were published in Volume III of the journal (1839, pp. 82–85, Plate 5, Figures 2–9). In addition to the small fins and the "bouton terminal", Blainville described the internal shell, which is covered dorsally and ventrally by thinner, oval parts of the mantle (p. 377). Blainville states that *Spirula* has two gills and that the intestinal tract is situated left of the shell, the ovary on the right. The nidamental glands are not mentioned in the text but are clearly visible in Figure 6; Figure 8 clearly reveals the insertion of the musc. retractor capitis on the margin of the last chamber of the shell.

Another well-preserved specimen of *Spirula* is described by J. E. Gray (1845, p. 257, Plate 15,
416 Figures 1–4). The specimen, which had lost only the clubs of the tentacles, belongs to the museum of Hugh Cuming, who had obtained it from Percy Earl of New Zealand; it was found there on the beach of Port Nicholson.

The specimen illustrated by Gray was described three years later by Owen in the *Zoology of H. M.*

* In the first edition of Péron's report, *Spirula* appears as "*Spirulea prototypos*" on Plate 30, Figure 4. Since this edition was published in 1807 while Lamarck's *Encyclop. method.* (Plate 465) appeared only in 1816, the species name "*prototypos*" has priority over "*australis*". (Note by A. Brauer.)

S. Samarang (Plate 4, Figures 2, 8). The report of the expedition also includes a description of a damaged specimen collected by Captain Sir Edward Belcher "in the Indian Archipelago" (Plate 4, Figures 1, 4, 5, 6, 11–15). In this specimen, which he named "*Sp. peronii*", Owen found a funnel valve, a salivary gland, a divided liver, and a funnel cartilage. Owen also described in this treatise a form which he named "*Sp. reticulata*" (Figures 3, 9, 10). The specimen was found near Timor and was handed to Owen, so that he might study it, by G. Bennett. It consisted only of mantle, shell and posterior end.

As to the 3 species described by Owen, he named the specimen caught by Péron, which has no terminal disc, "*Sp. peronii*", and all specimens that have a terminal disc "*Sp. australis*".

As regards *Sp. reticulata*, I shall refer to it later, proving that it is not a new species but only a form in which—due to the chafed off skin—the peculiar reticulate pattern of the surface of the musculature has come to the fore. Intact specimens do not show such a reticulate pattern.

An intact specimen of *Spirula* was caught in 1865 near Port Jackson on the south Australian coast by Angas (*Proc. Zool. Soc.*, London, 1865, p. 157). Angas expressed his surprise that live *Spirula* are so rare, though shells are being found in large numbers on islands and coasts in the area of the warm current. Regarding his catch, he merely states: "On one occasion only I had the good fortune to meet with the perfect animal enclosing the shell; it was thrown up, after a severe storm, on Bondi Beach, near Port Jackson, and it is now preserved in alcohol in the Sydney Museum."

The first detailed anatomical description of *Spirula* was presented by Richard Owen (1879). His description will be discussed later and we note here only that it was based on the specimen from the collection of Hugh Cuming which had already been described by Gray (1845) and by Owen himself. This was a female, and one year later, in 1880, Owen described the only male *Spirula* known until now. This specimen, purchased by the British Museum, was reportedly caught on the trip of the *Bonite*, although Souleyet ("Voyage autour du monde sur la Corvette la 'Bonite'", *Zool.*, Vol. II, p. 8) expressly notes that he failed to find any *Spirula*. Owen's description is, unfortunately, rather cursory, but it does state that hectocotylization affects both ventral arms. These arms bear no suckers and are longer than the other arms; the left arm is shorter than the right one, the latter being coiled at the tip.

The gonoducts are apparently situated on the right side and end in a short penis.

In his work *Sepiadarium og Idiosepius*, J. Steenstrup (1881) makes some remarks on fragments
417 of specimens in the Paris and British museums. He confirms Owen's description of the hectocotylization and considers *Spirula* as the closest relative of *Idiosepius* because it shows a similar type of hectocotilization. For the same reason he considers *Spirula* as belonging to the Myopsida and places it in the group Sepio-Loliginei which includes all Myopsida with hectocotylized 4th arms. Steenstrup's view on the systematic relationships of the Sepio-Loliginei is laid out in the following table:

Sepia	*Sepia* L., *Sepiella* Gray, *Hemisepius* Steenstr. *Sepiadarium* Steenstr., *Sepioloidea* d'Orb. *Idiosepius* Steenstr., *Spirula* Lamarck
Loligo	*Sepioteuthis* d'Orb., *Loligo* Lamarck *Loliolus* Steenstr.

The *Sepia*-like forms are classified by the form of the fins, as follows:

Eusepii: *Sepia*, *Sepiella*, *Hemisepius*,
Sepiadarii: *Sepiadarium*, *Sepioloidea*,
Idiosepii: *Idiosepius*, *Spirula*.

Even before the studies of Owen and Steenstrup were published, the *Challenger* Expedition had caught another specimen of *Spirula*, namely at its Station 194a, near Banda (29 September, 1874, 4°31′ S, 129°57′20″ E, 360 fath. Volc. mud., one specimen, with soft parts). Hoyle reports this catch in his *Report on the Cephalopoda* (1886, Vol. XVI, p. 122). The specimen was given to Huxley for study, but his paper was published only in 1895.

Meantime, A. Agassiz, too, had caught a specimen of *Spirula*, namely on board the *Blake*, near Grenada in the Caribbean Sea (*Bull. Mus. Comp. Zool.*, Cambridge, Mass., Vol. V, 1879, p. 298). In his comprehensive report on the travels of the *Blake* (*ibid.*, Vol. XV, 1888, p. 61), Agassiz illustrates the animal with opened mantle cavity, showing that it is a female (Figure 280). Unfortunately, further publications on this specimen are not available because, as Agassiz himself informed me, it disappeared from the collection.

Next, Giard (1893, p. 886) reported on two damaged specimens of *Spirula* of unknown origin, found in the possession of a captain in Nantes. Giard procured these specimens for the museum and handed them to Pelseneer, who was engaged in the publication of Huxley's work on *Spirula*.

Huxley's study of the specimen collected by the *Challenger* Expedition was finally published in the *Challenger* reports (1895), simultaneously with its French translation (in the *Bullet. Scientifique*). The plates were prepared by Huxley; the text, including the data obtained from the two specimens sent to him by Giard, was edited by Pelseneer.

Huxley and Pelseneer's description of *Spirula* will later be discussed in detail, but I would emphasize already at this point that Pelseneer (p. 46) is convinced that *Spirula* belongs to the Oegopsida.

418 Lönnberg (1896), on the other hand, places *Spirula* in the Myopsida; he came to this conclusion after having examined an intact specimen in the Zoological Museum in Upsala. This specimen was found floating on the surface by Captain C. Eckman near Madeira (43°30′ N, 16°3′ W). Lönnberg did not make a complete anatomical study, but only a histological examination of the mantle and aboral pole. He identified the specimen as *Sp. reticulata* and attempted a definition of the specific characters of the species known at the time. In the following table I have summarized the diagnoses of the 4 species as given by Lönnberg on the basis of earlier descriptions.

Spirula péronii	Mantle 52% of length of body. Absence of groove between terminal disc and mantle. Fins well developed. Ventral arms separated.
Sp. australis	Mantle 36% of length (male). Groove separating terminal disc and mantle. Fins weak. Ventral arms separated.
Sp. reticulata	Arm formula: $\overset{\frown}{3\;4}$, 2, 1. Groove separating terminal disc and mantle. Surface of mantle has reticulate pattern. Fins well developed. Ventral arms separated.
Sp. blakei	Groove separating terminal disc and mantle. Surface of mantle smooth.

	Fins well developed.
	Tentacles longer than body and head.
Sp. blakei (contd.)	Ventral arms connected by seam.
	Mantle twice as long as wide.
	West Indies.

The table shows that almost each specimen of *Spirula* caught by any expedition or obtained by exchange was given a different name. Closer examination of all the characters which LÖNNBERG—following earlier authors—adduced to distinguish the different species convinced me, however, that they are not valid.

As regards the proportion between the width and length of the mantle is a relative character which should certainly not be brought forward in the distinction of species. Thus, the sac-like, relatively wide shape of the mantle of the *Challenger* specimen of *Spirula peronii* is merely due to strong contraction, which causes the head to retract into the mantle to such an extent that only the arms project beyond the margin of the mantle. Where this is not the case, the animal appears more slender.

According to LÖNNBERG, a groove between mantle and terminal disc is absent only in *Sp. peronii.* He therefore uses this character to distinguish between *Sp. peronii* and the other species.

419 This groove is, however, less marked if the body is strongly contracted so that it is almost entirely enclosed by the mantle. This character has thus no value for the distinction between species.

The most important character presented by LÖNNBERG—the only one being at least potentially valid for the distinction of species—concerns the ventral arms. LÖNNBERG assumes that they are either connected by outer membranes or lack such membranes altogether. His conclusion that outer membranes are present in *Sp. blakei* is based on the illustration of AGASSIZ which was also copied by PELSENEER. The drawing of AGASSIZ, however, is unclear in this very point, because what LÖNNBERG considers to be a membrane may very well be the contours of the buccal apparatus that is shining through, which was presented by the artist as soft outlines set off against the membraneless ventral arms. In any case, such an ambivalent drawing can certainly not be adduced for the establishment of a new species.

As to *Sp. reticulata*, finally, I have already pointed out that the reticulate pattern of the surface is present only in specimens in which the body epithelium and the subcutaneous connective tissue on the mantle were chafed off. In my specimen, the reticulate pattern is distinctly visible on the mantle surface. It is however absent wherever parts of the subcutaneous connective tissue or the entire skin are well preserved. I can therefore not agree that a species should be established on the basis of a character visible only due to an injury.

All other characters mentioned by LÖNNBERG and earlier authors are relative characters and not specific differences. Such characters are the relative length of the tentacles, the relative size of the fins and the relative width of the mantle.

I conclude, therefore, that all specimens of *Spirula* with soft parts collected until now belong to a single species. This species might be named *Sp. australis*, as proposed by LAMARCK.

I published this opinion in a communication on "*Spirula australis* LAM." (1910), in which I presented a summary of the results obtained from our specimen.

In the same year there appeared the first report on a larva of *Spirula* (JOUBIN, 1910). It was caught with a submerged plankton net at a depth of 3,000 m near the Canaries on a voyage of the *Prince of Monaco* in 1904.

In view of the interest of this pelagic juvenile stage, it is worth mentioning that I found 4 larvae

of *Spirula* in the material collected by the *Michael Sars* Expedition under the direction of Johan Hjort. I described these larvae, and older specimens collected by the same expedition, in the Report on the North Atlantic Deep-Sea Expedition (1913). In the present work, these larvae are described and illustrated (Plate LXXI) by courtesy of J. Hjort. All larvae and older specimens were collected in the Canaries Current, which is apparently a classic area of *Spirula*.

420 2. Form of body

Mantle

The **mantle** is strong, cylindrical, 400 mm long, and 18 mm wide in the middle. The length is measured from the dorsal mantle corner to the posterior disc; the lateral length of the mantle is 31 mm from the base of the fins to its border, below the eyes. The dorsal mantle corner is spatulate and extends to the level of the middle of the eye. The ventral corners, too, project markedly; they surround the funnel with a rounded indentation and adhere firmly to it with their posterior and middle margin (Plate LXIV, Figure 1). The mantle is strongly muscular, up to 1.5 mm thick, but it becomes thinner toward the projecting ventral and dorsal margin of the shell, loses its musculature, and forms a thin lamella which Owen named "periostracum". The chambers of the shell are visible through these two ovals, which have been observed by all earlier authors. They are bordered anteriorly and laterally by the muscular parts of the mantle which are slightly swollen and pass posteriorly gradually into the terminal disc. The dorsal oval is slightly larger than the ventral one (Plate LXVII, Figure 1, *d.*, *v.*), 12 mm long and 7 mm wide. The swollen, cheek-like posterior margins of the muscular part of the mantle are sharply differentiated from the terminal disc (Plate LXIV); that is, they form here a groove which borders on the terminal disc to the base of the fins and is sharply incised between the outer base of the fins and the mantle margin.

This description shows that the shell is completely enclosed by the mantle; the latter is peculiar only in that it becomes markedly thinner in the so-called "ovals" between the dorsal and ventral margin of the shell. Earlier observers, particularly Blainville (837, p. 377), already proved that this is an internal shell. The thin part of the mantle (Owen's "periostracum", 1879, pp. 2, 3) is delicate and very prone to chafing by the net. This was the case with the *Challenger* specimen, Huxley's illustration of which clearly shows the damaged mantle areas along the ovals. Even if this so-called periostracum is intact, the translucent shell may give the false impression that it is not covered by the mantle, at all. This fact induced Pelseneer (1895, pp. 12, 13) to consider the shell of *Spirula* as external. Pelseneer attempted to demonstrate by diagrammatic drawings how, in the course of development, the external shell becomes covered by two lateral lobes of the mantle, so that the dorsal and ventral sides of the shell remain free. He thinks that these lobes approach and contact each other at the posterior end of the body and finally fuse to form the terminal disc. He maintains that "il n'y a aucune portion des téguments, si mince qu'elle soit, qui passe au-dessus de la coquille"; but I can stress that in our specimen, in which the periostracum on the ventral oval was also torn, the thin lamellae on the shell are quite distinct.

The shell of *Spirula* is thus internal, which is proved not only by a careful examination of the
421 adult but also by the condition of the larves, a condition which Joubin (1910) was the first to report. Later (1912), I found larvae of the same age as well as older larvae in the material of the *Michael Sars* Expedition (Plate LXXI). Just as Joubin found in his larva, all these specimens show that the shell is covered with a shell sac equipped with chromatophores. The shell sac is part of the mantle; at an early age the mantle becomes very thin near the shell (Plate LXXIII, Figure 1).

Except for the posterior end, the mantle was chafed and the epithelium and cutis were lost (Plate LXIV, Figure 1). The mantle thus shows almost everywhere the reticulate structure caused by protruding ridges (Plate LXVI, Figures 1, 2). OWEN accordingly named the species *Sp. reticulata*. The mesh of this network is larger in the posterior part of the mantle than anteriorly; between the widest meshes there are the weaker reticulate ridges.

The **fins** are situated transversely at the posterior pole of the body, at the border between the swollen mantle margin and the terminal disc (Plate LXIV, Figure 3). The base of the fins is 9 mm wide and extends from the dorsal to the ventral oval. The distance between the dorsal bases of the fins is 8 mm, that between the ventral bases 5 mm. The fins are thus not exactly horizontal but converge slightly toward the ventral side. That they are not fused at the posterior end of the body is due to the peculiar transformation of this end into a characteristic organ, which was first observed in 1836, by ROBERT.

This **terminal disc** ("bouton terminal") of the early authors consists of a protruding, slightly dorsally displaced circular swelling between the base of the fins (Plate LXIV, Figure 3). It is 9 mm wide and 2.5 mm thick. The terminal disc ends gradually, without forming a groove toward the ovals (Figure 1); but a deep constriction separates it from the base of the fins. The peripheral circular swelling of the terminal disc borders a deep pit from the center of which projects a conical formation, the so-called terminal papilla.

Various authors presented very different interpretations of the fine structure and probable function of this formation, and this will be discussed in detail in a special chapter.

Funnel apparatus

The **funnel** projects only slightly from the circular indentation of the ventral mantle corners. Anteriorly it continues in a narrow tube which contains a valve in front of the opening (Plate LXV, Figure 4). Toward the mantle cavity it widens rapidly to a slightly concave, sharp posterior margin. (*ibid.*, Figures 1, 2). Laterally it bears two large funnel cartilages (Plate LXVII, Figures 1–3, *cart.*) on which the collaris is broadly inserted. These cartilages have laterally overlapping margins and are rather flat, 7 mm long and 3 mm wide. Into their groove-shaped depression fits the mantle cartilage which is 8.5 mm long; posteriorly it slightly widens and flattens. The anterior end of the mantle cartilage does not approach the mantle margin.

422 The outer part of the **collaris** (Plate LXIX, Figure 1, *coll.*) forms a closed ring and is attached to the dorsal middle of the lower side of the well-developed neck cartilage (Plate LXV, Figure 3); the latter is 7 mm long and 3 mm wide and resembles the sole of a shoe, as it is constricted in the anterior third. The fibers of the collaris are broken by an anterior triangular cartilaginous indentation which HUXLEY (1895, Plate I, Figure 5) illustrates as constituting all of the cartilage. The dorsal mantle cartilage, which fits into the groove of the neck cartilage, forms a ridge which disappears toward the dorsal corners of the mantle.

If the funnel is opened by a ventral median incision, it shows the **funnel organ** (Plate LXV, Figure 4), which PELSENEER (p. 8) expressly failed to see. It resembles that of most Myopsida and consists of a single, heart-shaped dorsal part (*org. inf. m.*) the tip of which is directed anteriorly and the posterior margin of which has a deep indentation. Its paired ventral parts (*org. inf. l.*) are situated more anteriorly; they are oval or pear-shaped. All 3 parts of the funnel organ are 4 mm long; the dorsal part is 4.5 mm wide.

Head

The **head** is short and wide, and the neck tapers toward the collaris. It is 12 mm long from the anterior margin of the funnel cartilage to the base of the ventral arms, and 20 mm wide. The width of the head is caused by the large eyes. The olfactory tubercles are distinct at the ventral base of the head, in front of the funnel cartilages (Plate LXV, Figure 2; Plate LXIX, Figure 1, *olf.*). They are knob-shaped and measure 1–1.2 mm. They were first illustrated by HUXLEY.

The **eyes**—like those of all Oegopsida—are open, covered only by a lid fold. The lid fold in our specimen contracted to a small, oval or pear-shaped pupil, 2 mm wide, lacking a distinct sinus lacrimalis. A lid muscle extends anteriorly and slightly ventrally from the fundus of the eyeball and forms a large circular muscle along the inner lid margin. The right eye will be thoroughly described later. The eyeball is slightly oval, 10 mm wide and 11.5 mm long. The lens is large, 5 mm wide. The posterior half of the eye is slightly larger than the more rounded anterior half. The lens-shaped optic ganglion (Plate LXIX, Figure 2, *g. opt.*) is 6.5 mm long and 4 mm wide; it borders on the posterior side of the eyeball and on the ring-shaped, relatively small, white body.

Arm apparatus

The arms and tentacles of our specimen are well preserved.

The **arms** (Plate LXV, Figure 5) are relatively short and strong; they differ only slightly in size.
423 Since the longitudinal muscle cords which enter the base of the arms can be followed to the level of the eyes, the distance from the proximal suckers to the tips of the arms is a more reliable measure of the length of the arms. The 1st arms are 7.5 mm long, the 3rd arms 9 mm, and the 2nd and 4th arms are 9.5 mm long, so that the formula is $\overset{\frown}{2\;4}$, 3, 1.

The inner side of all 8 arms bears numerous longitudinal rows of suckers. The longitudinal and oblique rows of suckers are not very distinct, but there are about 4 longitudinal rows from the middle of the arm onward. Toward the base, the number of suckers in the oblique rows increases to 8 on the 1st arms and to 6 on the other arms. The number of suckers decreases rapidly to two at the base.

The suckers of the arms have short stalks and a hemispherical dorsal surface. The inner surface of each sucker, up to the central muscular pad, is strongly chitinized. Toward the outside, this chitinous layer passes, as usual, into a chitinous membrane which had rodlike indentations.

The midpart of the membrane has about 4 rows of polygonal areas, each with a tubercle. The proper denticles of the suckers are situated innermost, around the opening; they are bluntly conical; the median ventral tooth is larger than the lateral teeth.

The **membranes** of the arms will be described in detail, because they have hardly been mentioned by earlier authors.

The rows of suckers are surrounded by not very wide but strong **protective membranes** which extend from the base to the tip. The arms are connected at the base by strong **outer membranes** which continue for some distance along the outer edges of the arm. The outer membranes are shortest between the first two arms and increase in width, also extending further, toward the 3rd arms. They are absent between the ventral arms (Plate LXVI, Figures 3, 4). This is apparently a character of all specimens of *Spirula*, including the specimen collected by the *Blake* (see p. 323), for which LÖNNBERG stated that there is a short outer membrane between the ventral arms.

There is also an **inner membrane**, namely between the 2nd and 3rd arms; together with the outer membranes it forms a sheath from which the tentacles project. **Swimming membranes** or keels are

moderately developed only on the 1st arms; those of the 2nd and 3rd arms are weakly developed and restricted to the distal part. The ventral arms have no keel, but the outer membranes that surround the tentacles continue for some distance as sharp edges.

The **tentacles** of our specimen are well preserved and partly retracted. They project 19 mm on the right and 23 mm on the left side. Opening of the orbit shows their lyre-shaped root the inner margin of which is approached by a broad lamella. Inside this lamella passes the tentacle nerve and a larger vessel.

424 The right tentacle, including its basis, is 41 mm long, though it was strongly contracted. This proves again, as noted above (p. 418), that the relative length of the tentacle cannot be used as a specific character. The tentacles are cylindrical at the base and continue then flattened on their inner surface; this inner surface is separated from the rounded outer surface by two ridges and narrows very gradually toward the club. The tentacle stalk passes into the club without widening; rather, it tapers to the tip.

The **club** (Plate LXV, Figure 6) is only slightly widened; it is 7 mm long and 2 mm wide; at the tip it is slightly curved dorsally; it bears a long keel which is displaced dorsally and resembles a protective membrane. The dorsal protective membrane is very narrow, whereas the ventral one is very wide, even slightly wider than the keel. As noted already by earlier observers, the club bears numerous small suckers, arranged in indistinct longitudinal and oblique rows. There are about 1–12 suckers in an oblique row in the widened middle part of the club; the proximal and distal rows bear far fewer suckers.

Coloration

A color dawing (Plate LXIV), made immediately after collection of the animal, shows its purple-violet tone. I found no evidence of the intense pink coloration of the arms described by PÉRON for his specimen. The mantle was chafed, so that it revealed only the weakly flesh-colored tone of the musculature, the purple to brownish coloration being apparent only at the head, the arms and the posterior end of the body, near the fins. Since this seems to have been the color of the intact mantle, I have portrayed this color in Figure 2 as an attempt to show the overall coloration of the animal, while Figure 1 portrays the freshly captured specimen.

The tentacles are of a weak flesh-pink; nor is the color of the club more intense. Opening of the mantle cavity shows that the purple color extends to the anterior inner margin of the mantle (Plate LXV, Figure 1), and continues on the funnel to the anterior margin of the closing cartilage (Plate LXVII, Figures 2, 3). The remnants of the subcutaneous connective tissue which were preserved in the posterior parts of the mantle showed a silky sheen.

The coloration is caused mainly by **chromatophores** in the cutis (Plate LXX, Figure 5). The connective tissue recedes around the chromatophores, so that they are situated in cavities. Otherwise the structure of the chromatophores closely resembles that of other Cephalopods. The pigment is granular and yellowish brown in younger chromatophores, darker in older ones. There is a large, oval nucleus in its middle. The smaller nuclei are arranged in a circle at the margin of the chromatophores, mainly at the base of the contractile processes. The outer surface of the chromatophores shows a light,
425 honeycomb-like layer which gradually disappears near the insertions of the muscles. At all the colored areas the chromatophores are stacked densely, in several superimposed layers, but at both sides of the fins they are sparse, and at the margin of the fins they disappear altogether.

The purple coloration is caused not only by the chromatophores but also by a finely granulate pigment in the subcutaneous tissue, mainly in the area of the terminal disc. The pigment consists of

spherical or oval flakes near the nuclei of the loose gelatinous subcutaneous tissue; there are either a few large flakes or more numerous smaller flakes (Plate LXX, Figure 14).

Some remarks on the coloration of the specimens caught by the *Michael Sars* Expedition should be of interest; they concern only the older stages, since the younger specimens will be described later. A young specimen of 12 mm mantle length (Plate LXXI, Figure 7) shows a strong pigmentation on the head and the posterior end of the body (Figure 8); the terminal disc is just about to develop amidst the fins; its cupola is almost completely devoid of chromatophores, especially near the whitish terminal papilla. The mantle is only weakly pigmented; since it was slightly damaged, the artist showed the distribution of chromatophores arbitrarily.

What is certain is that in slightly older stages the pigmentation in the middle of the mantle disappears almost completely, while the head, mantle margin and end of the body become more intensively pigmented. This is shown in the photograph of a young *Spirula* of 16 mm mantle length (Text Figure 35).

The photograph shows the concentration of chromatophores in the posterior part of the body, near the shell which shows through. Toward the middle of the mantle the chromatophores become sparser and almost completely disappear. Only the margin and corners of the mantle show chromatophores, namely in the form of a dark seam. The fins are devoid of chromatophores, except at their base, and so is the cupola of the terminal disc with its whitish terminal papilla.

Due to the absence of chromatophores on the median part of the mantle, the silky cutis here shines through. It consists of loose, undulate bands, extending in the longitudinal axis. The transparent epidermis of a specimen of the same size and from the same station was torn at some points, so that the brilliant sheen of the silky strands of the cutis were visible.

FIGURE 35. *Spirula* juv. Dorsal mantle length 16 mm. Head retracted; the swelling in the anterior part of the mantle is caused by the eyes. The posterior end of the body shows the terminal papilla. Ventral view.

FIGURE 36. *Spirula* of 23 mm mantle length. The epidermis of the mantle is chafed away, showing the silky cutis. Dorsal view.

426 This silky or silvery sheen of the cutis was observed also in a younger *Spirula* of 23 mm mantle length the epidermis of which was almost completely chafed away, so that part of the shell at the dorsal oval was exposed. I present an illustration of this specimen (Text Figure 36), because its head projects free from the mantle, while that of the former specimen was almost completely retracted. The head—especially the large eyes and the base of the arms—is dotted densely with small chromatophores which are light-brown, with an orange tinge. They probably cause the white-coffee coloration of the live animal reported by Robert (1836) for the specimens from the Canaries.

The posterior part of the body has a similar coloration as the head; otherwise it resembles that of the specimen shown in Text Figure 35.

The characteristic reticulate pattern of the surface of the mantle is present in all specimens in which the cutis is partly detached from the muscular layer. In juvenile specimens the mantle surface is rather granulate, the reticulate pattern becoming distinct only in older specimens. This particularly applies to the largest specimen of the *Michael Sars* Expedition. It has a dorsal mantle length of 26 mm and is severely damaged, so that the cutis is lost. *Spirula* is apparently very delicate, so that its skin is more liable to become detached than that of other Cephalopoda. This may be due mainly to the fact that the lamellae of the cutis adhere only loosely to the musculature. If the thin, transparent epithelial layer separates from the cutis, the silvery strands of the latter swell and sever in loose bands. This iondition is illustrated in Text Figure 37 which shows a *Spirula* of 17 mm mantle length. It shows the transparent epithelial layer which has severed in separate lamellae, as well as the loose, undulate silvery bands of the cutis.

3. Mantle complex

(Plate LXV, Figures 1, 2; Plate LXVI, Figures 3, 4; Plate LXVII)

Upon opening the mantle cavity by making a median ventral and a circular incision around the ventral oval one notes how closely the topography of the mantle complex resembles that of the Myopsida.

The **funnel** is visible its entire length, from the tapering, chimney-shaped anterior part to the broad posterior part whose sharp, thin posterior margin forms a slightly concave curve. The cartilages of the funnel and mantle are distinctly visible. Anterior to the funnel, the head tapers toward the collaris
427 into the neck; the two light-colored olfactory tubercles are situated on its ventral side, just anterior to the funnel cartilages (Plates LXV, Figures 1, 2, *olf.*).

The **musculi depressores infundibuli** (Plate LXVII, *mu. depr.*) are thick, 6.5 mm long and 3 mm wide; they extend toward the single funnel organ, into the dorsal wall of the funnel (Plate LXV, Figure 4, *depr. inf.*). They flatten posteriorly and form a somewhat blunt edge overlying the muscle cords, at about half the height of the gills (Plate LXVII, Figure 2). These cords belong to the lateral parts of the liver which is present in most Myopsida. Deeper dissection shows that the cords comprise a completely closed ring (Plate LXVIII, Figure 3), formed dorsally by the musculus retractor capitis medianus, laterally and ventrally by the musculus retractor capitis lateralis (Plate LXIX, Figure 1, *mu. hep.*). These muscles are not sharply differentiated from each other but are confluent; they are inserted on the anterior margin of the shell sac, where it curves into the concavity of the last chamber (Text Figure 38).

Brock (1880, p. 21) described a completely closed muscular liver sac formed by the retractors in
428 *Sepiola*. These conditions were described inadequately for *Spirula* by earlier authors, especially Owen and Pelseneer. This may be the occasion to correct an error of Owen, namely that the nervus pallialis perforates the depressor infundibuli. This is certainly not the case, because the pallial nerve laterally

a

a

b

FIGURE 37. Young *Spirula* of 17 mm mantle length.

a dorsal view, ventral view; b lateral view. The mantle epithelium has become detached and severed in broad lamellae; the underlying cutis has separated at some points, forming silvery, undulate bands.

and slightly dorsally penetrates the muscular capsule of the liver, about 3 mm from the margin, without contacting the depressor which is situated ventrally (Plate LXIX, Figure 1, *n. pall.*). The parts of the liver capsule which surround the entrance of the n. pallialis probably belong to the m. retractor capitis medianus.

The two **gills**, which were first described to Blainville, are of medium size (Plate LXVII, Figure 2). They are 9 mm long and 4–4.5 mm wide. Anteriorly they are pointed, are widest in the middle and slightly narrower posteriorly. The alternating inner and outer branchial lamellae do not differ markedly in size, but the inner lamellae are slightly wider (up to 4 mm). There are 25 inner and 25 outer lamellae. This agrees with the observations of Owen (1879, p. 12) who found 24 lamellae. The branchial vein passes as usual on the crest of the gill, receiving smaller vessels, and then bends at the base toward the atria. The branchial lamellae are attached by parallel lamellae to the branchial gland which is covered by the overlapping inner branchial lamellae and therefore not visible from the outside. The branchial gland extends along the whole outer margin of the gill and forms the insertion for the ligament. It is broad and strong (Plate LXV, Figure 2) and extends with its insertion on the mantle obliquely from the stellate ganglion to the level of the funnel cartilage.

The vena cava passes in the median line and can be seen behind the heart-shaped part of the single funnel organ, together with the visceral nerves which approach each other, almost touching, in front of the anus where they are connected by a commissure.

The arrangement of the organs of the mantle complex is influenced markedly by the chambered **shell** which has an endogastric siphuncle. The shell is situated in the median plane of the posterior end of the body, so that on opening the mantle cavity one encounters its narrow outer side. About 4 chambers are visible from the outside; they show through because the mantle is very thin in the area of the transparent oval, where the shell is contiguous with the mantle. If the terminal chamber is numbered 1, chambers 7 to 10 are visible from the ventral side. If the mantle lobes are folded back, the other chambers, which are covered by the thick and densely vascularized shell sac, become visible (Plate LXVII, Figure 2). Deeper dissection shows that the shell sac curves back at the margin of the terminal chamber and lines its concave inner surface. The retractors which form the muscular capsule of the liver are attached to its back-folded margin (Text Figure 38). On opening of the shell one sees the spindle-shaped, endogastric siphonal necks (Plate LXVII, Figures 2, 3).

Only few parts of the **intestinal tract** can be seen on opening the mantle cavity, among them the anus which is situated 2 mm from the posterior margin of the funnel (Plate LXVII, Figure 2). Its
429 dorsal and ventral lips are fleshy, and the usual anal appendages are apparently absent. However, closer examination shows that they are present as short, knob-shaped tubercles at the lateral margin of the lips. The rectum extends slightly obliquely posteriorly, then forms a loop to the left and passes into the mid-intestine. There is also a caecum, situated left of the shell and enclosed in a delicate sac together with the pancreatic appendages (Plate LXVII, Figure 3).

Excretory system. The two chimney-shaped renal papillae (*ur.*) are distinctly visible on the right and left sides behind the anus. The *Spirula* specimen caught by the *Blake* Expedition seems to resemble ours in this respect. In the *Challenger* specimen, however, this chimney-like projection of the papillae was less marked. I do not agree with Pelseneer, who thinks that this condition shows a relationship between *Spirula* and the Oegopsida. It may be sufficient to stress that the proximity of the chimney-shaped renal papillae to the rectum is an unmistakable character of the Myopsida. The renal sacs with their thin appendages are visible indistinctly through the abdominal wall. From the renal papillae onward, the renal sacs widen toward the base of the gills, reaching 10 mm. Opening of the renal sacs (Plate LXVII, Figure 2) reveals the venous appendages; the intestine passes through them. Contrary

to Pelseneer, who considers these appendages as completely separate sacs, we shall show that they broadly communicate with each other in front and behind the intestine.

The topography of the mantle complex obtains its characteristic formation by the **genitalia** with their efferent ducts and accessory glands. Our specimen is a mature female. It has two pairs of distinct nidamental glands (Plate LXV, Figures 1, 2, 4) which are situated symmetrically on the ventral surface of the abdominal wall and extend from the renal papillae quite some way beyond the base of the gills. The nidamental glands are large and cover the greater part of the renal sacs and the adjacent organs. They consist of the nidamental glands *sensu stricto* and the accessory nidamental glands (*nid. acc.*), situated dorsally to the former. The nidamental glands have the form of a coffee bean and show a distinct radial arrangement of lamellae around a central slit which separates the two arms of the gland that are fused posteriorly. The accessory nidamental glands are heart-shaped; they form two broad, diverging arms posteriorly, where they are covered by the nidamental glands. The outer arms are slightly larger than the inner ones. All glands are 3 mm long and 2.3 mm wide.

4. Shell sac and formation of the shell

(Plates LXXII, LXXIII)

As stated above (p. 324), the shell of *Spirula* is completely enclosed by the mantle and is situated entirely inside the body. This applies in particular to the two transparent ovals on the ventral and dorsal
430 side of the body which turned out to be thinned parts of the mantle. Already Blainville recognized that the shell is internal, contrary to later authors, especially Pelseneer, who considered the shell as external, secreted by the mantle. Owen (1879, p. 11) stressed correctly that the shell is enveloped by the shell sac, in the same manner as the internal shell of the Sepiidae. According to Owen, the shell sac covers not only the outer wall of the shell, where it passes into the proostracum (the ovals), but also lines the inside of the living chamber, from the insertion of the head retractors and the funnel depressor onward, finally ending in the siphuncle. According to Pelseneer, who considers the shell as external (1895, pp. 19 and 35), a shell sac does not exist at all, as in his opinion it is the surface of the mantle that forms the shell, namely there where it adheres to it.

My studies have shown that there is a completely closed shell sac which adheres to the outer wall of the shell, bends around the margin of the living chamber, adheres to the last septum, and continues in the siphuncle. The siphuncle is a cord-shaped continuation of the shell sac inside the shell. Its surface is covered with epithelium and contains numerous capillaries. For the terminology of the shell sac, it seems advisable to use the terms which Appellöf and other recent observers used for the shell.

The chambered shell is situated in the median plane and is curved like a post horn, with a convex outer or dorsal surface and a concave inner or ventral surface (Plate LXVII, Figure 1). The younger chambers, i.e. the last-formed ones, are situated on the dorsal side, contiguous with the dorsal oval. The older chambers decrease in size as they approach the ventral side, i.e. the ventral oval; from here they extend, curved in post horn form, into the initial chamber in the middle of the body, where they end. The siphuncle is situated so close to the ventral side that the lumen of the chambers is reduced to a slit on the concave ventral side. The septa surrounding the siphuncle extend posteriorly into cambered necks and project into the opening of the preceding neck with whose walls they fuse by means of a pillar substance, so that the siphuncle is enclosed its whole length by a calcified tube. This terminology of the shell provides analogous terms for the shell sac, which has a convex dorsal surface, a concave ventral surface, a shell margin surrounding the margin of the living chamber, a lamella lining the living

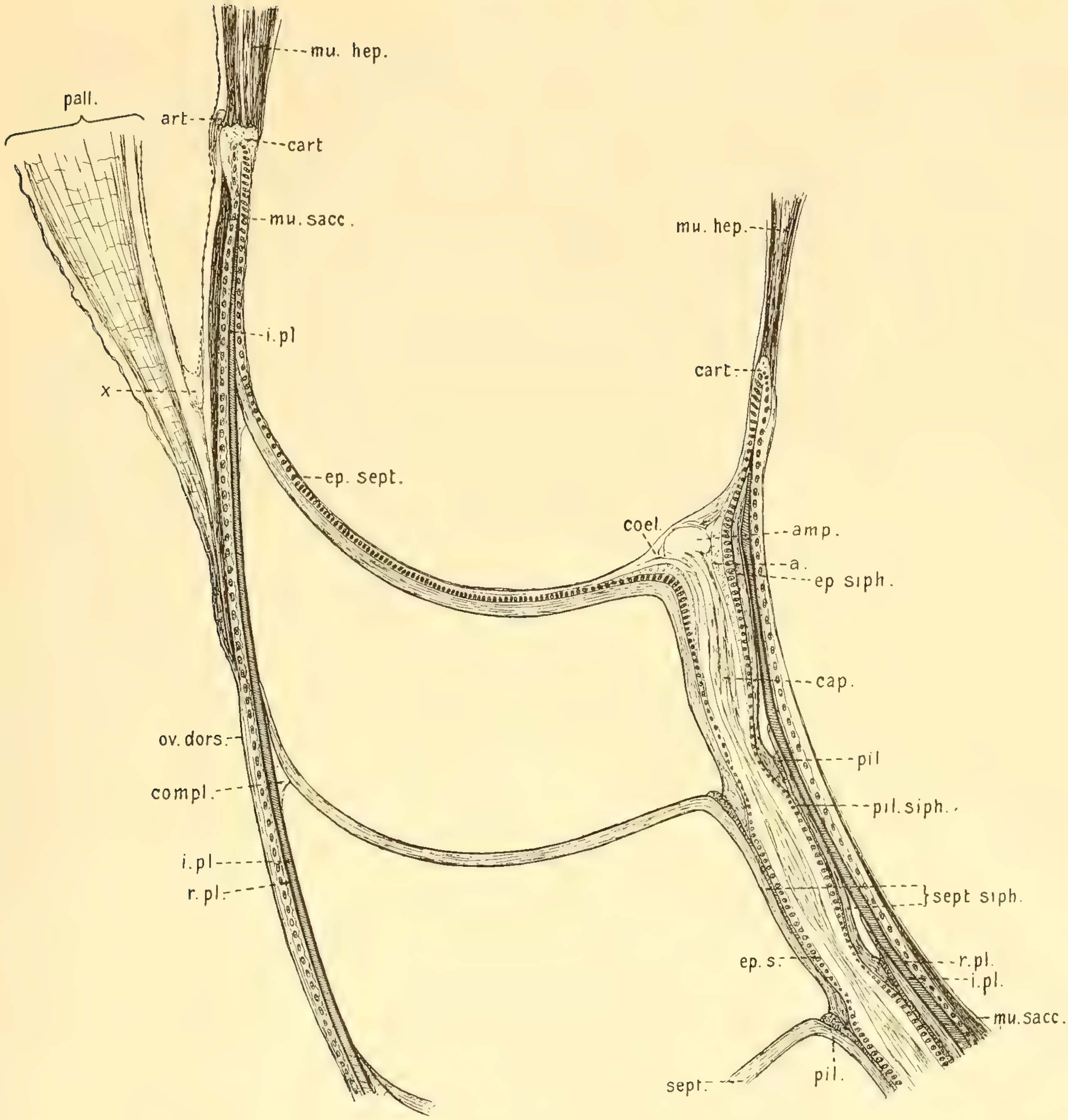

FIGURE 38

chamber, and a siphuncle which extends ventrally from the living chamber. The shell sac is well developed as an independent formation in all the sites in which it does not border on the mantle; but it is fused with the mantle on its entire dorsal surface, from the penultimate chamber to the ventrally situated 20th chamber, so that at these sites it does not constitute an independent formation. This applies especially to the dorsal oval, the terminal disc and the ventral oval.

The first 10 chambers formed curve into a post horn, so that they approach the adjacent older chambers or volutions of the shell. This results in a fusion of the adjacent dorsal and ventral surfaces

431 of the shell sac. There is no dividing line between the thicker ventral wall of the older volutions of the shell and the thinner dorsal wall of the younger volutions in this central part of the shell. This uniform part of the shell extends to the "umbilicus", as the space between the initial chamber and the first volutions of the shell is called (in analogy to the shell of *Nautilus*); this space consists of about 7 chambers.

As regards the structure of the shell sac, we describe at first the outer surface (in contrast to the inner surface which lines the living chamber) which secretes the shell with what Appellöf termed its outer and inner plates. The basic materials for the morphology of the shell sac are comprised of a layer of connective tissue which partly adheres on its outside to longitudinal muscles while its inside is lined by the epithelium of the shell sac (Plate LXXIII, Figure 5).

In the anterior part of the shell sac the connective tissue contains bars or squamous elements (iridocytes) resembling those of the cutis of the outer skin. Posteriorly the connective tissue gradually assumes a finely fibrous structure the denser parts of which adhere directly to the epithelium. Inside the shell sac the fibers are loosely arranged and lie embedded in a gelatinous substance which contains capillaries. On the dorsal side of the shell sac, in the region of the living chamber, the connective tissue in every respect resembles the cutis of the inner surface of the mantle, since the epithelium of this cutis folds over onto the shell sac. In the angle between the mantle and the anterior end of the shell sac (Text Figure 38, *x*), the tissue is particularly loose and closely resembles the delicate layers of connective tissue which cover the stellate ganglia. Dorsally, the outer sheath of longitudinal muscles adheres to the shell sac only in the living chamber and in part of the penultimate chamber; ventrally it extends farther, to about the 4th chamber before the living chamber (Plate LXXIII, Figure 5).

The muscular layer is innervated by the mantle ganglia; just behind the margin of the living chamber, these ganglia send on each side a thin nerve to the shell sac. At the margin of the living chamber, the epithelium of the shell sac consists of cylindrical cells (Plate LXXII, Figure 3) which gradually pass posteriorly, into cuboid and, finally, flattened elements. These cells are, as indeed often observed in secreting epithelial layers, separated by light-colored lens-shaped spaces and show a fine fibrous structure at the base. Their nuclei are rarely spherical, usually of irregular form, or they are grossly ramified. The latter form is particularly distinct in the posterior part of the shell sac, where the nuclei are grossly ramified or sausage-shaped (Plate LXXIII, Figure 4).

In the area where the two lamellae conflow, the ventral lamella is much thicker than the dorsal one. The ventral lamella also bears a thick, fibrous layer of connective tissue which adheres to the epithelium. This layer of connective tissue stains strongly with eosin; in longitudinal section it is seen to continue as a strand into the 6th chamber, after which it loosens and divides into longitudinal fibers extending in the middle of the uniform sac. Dorsally, the connective tissue is looser; in the middle of the uniform sac, where blood capillaries are present, it assumes a gelatinous consistency. At their point of fusion, the two lamellae are covered by a thin layer of epithelium which apparently belongs to the
432 epithelium of the body cavity. Finally, it should be mentioned that on its convex dorsal side, the initial part of the shell sac, which is formed by the two fused lamellae, projects in the form of a saddles between each two chambers.

The initial part of the shell sac shows a noteworthy peculiarity; it has longitudinal folds which are lined by the epithelium of the shell sac and secrete chitinous lamellae (Plate LXXIII, Figures 6, 7). These folds first appear on the ventral surface, just behind the fusion of the two lamellae and extend to finally cover the whole surface, up to the initial chamber. The greatest number of folds is to be found at the 4th and 5th chambers, where longitudinal sections show 3 longitudinal folds. The chitinous lamellae between the folds ($ch.^3$) are finely striated; their calcification forms the longitudinal ridges on

the outer wall. The illustrations of the 4th (Figure 6) and 6th (Figure 7) saddles of the fused shell sac give an idea of the complicated condition of the shell sac in these areas. As to the 6th saddle, the shell wall of the 20th chamber shows 4 chitinous layers which are sharply defined because of their staining properties (*ch.*^{1}, *ch.*^{2}). The layer which corresponds to the "inner plate" (*i. p.*) bears radial thickenings. Then follows a 5th chitinous layer (*ch.*^{3}) which is covered on both sides with epithelium of the shell sac. On this layer is situated a thick, sharply defined layer of connective tissue (*bg.*) which extends into the ventral wall of the anterior part of the shell sac. The connective tissue becomes gelatinous in the middle (*ga.*) but it then becomes denser at the saddle. The epithelium (*ep.*), which covers the shell wall between the 6th and 7th chamber, consists of cylindrical cells, but I did not find a similar condition in the areas of the other saddles, including the 4th saddle (Figure 6) with its triply folded shell sac. On the other hand, the layer of the shell sac that penetrates into the saddle is surrounded laterally by a boat-shaped chitinous lamella which is open toward the wall of the shell sac.

The layer of connective tissue of the shell sac gradually assumes a slightly different structure toward the initial chamber. The fibers, which usually have a central nucleus, begin to pass through the uniform part of the shell sac in a dorsoventral direction (Plate LXXII, Figure 1, *sacc.*) and finally cross each other in various directions in the area of the umbilicus (Figure 2, *umb.*). The terminal branches of the capillary network (*v.*) and their nuclei are clearly visible in this gelatinous area. Sections through the lateral surface of the umbilicus show the well-developed epithelial layer (*ep.*) of the shell sac the nuclei of which are shown in Plate LXXIII, Figure 4. The numerous blood vessels and the perfectly developed epithelium in the initial part of the shell sac with the umbilicus contrast sharply with the adjacent areas of the degenerated siphuncle which will be described below. The perfect condition of the initial part of the shell sac indicates that the epithelium remains active for a long time and secretes new chitinous lamellae beneath the old one. As a result, the dorsal wall is unusually thick in the area
433 of the 1st chambers (Figure 2, *a. p.*). Decalcified sections do not show a sharp division into an outer and an inner layer (*i. p.*, *a. p.*) even in this thick part of the wall.

The **margin of the living chamber** (Plate LXXII, Figure 3; Text Figure 38) is supported by a cartilaginous ring (*cart.*) which appears in longitudinal sections as a clasp around the anterior margin of the shell. The cartilaginous ring is thicker on the dorsal outer surface than on the ventral surface,
434 which adheres to the inner margin of the living chamber. The cartilaginous ring not only strengthens the folded-over margin of the shell sac but above all serves as insertion for the muscular envelope of the liver (*mu. hep.*); the latter is completely closed and separated from the mantle. It consists of the musculus retractor capitis medianus and lateralis. The two muscles become fused without sharp boundary; however, the fibers of the two muscles can be distinguished by their oblique striation (Plate LXIX, Figure 1, *mu. hep.*).

The muscular sac of the liver is slightly thicker ventrally than dorsally, as shown by the cross section. The longitudinal muscles of the shell sac are inserted on the posterior margin of the cartilaginous ring; the ring is produced into a lamella.

Examination of the cartilage under [oil] immersion shows branched cartilage cells which are light-colored in contrast to the darker-staining intercellular substance of the cartilage. The nuclei of these cells with their irregularly distributed chromatin granules stain intensively and are rounded, oval or of irregular form. The substance of the cartilage has apparently sometimes a fibrous structure but this is never distinct and is present only at some points. Capillaries are present, especially near the epithelial layer. The abundance of capillaries in the other parts of the shell sac has already been mentioned above; the thin arterial branches originate from a thick vessel which passes through the liver perpendicular to the shell margin and enters into the dorsal median line of the shell sac just in front of the cartilaginous

ring (Plate LXVIII, Figure 3). This vessel apparently widens here into a semicircle and has thick branches to the dorsal wall of the shell sac. Before entering the shell sac, it has another branch which reaches the inner surface bordering on the living chamber. It apparently branches further, but a thicker vessel can be followed to the opening of the last siphonal neck where it swells slightly together with a few smaller vessels. The origin of the thick dorsal artery from the cephalic aorta or from the hepatic artery could not be followed more exactly.

The epithelium of the shell sac becomes cylindrical near the cartilaginous ring, especially where it is folded over toward the living chamber. Both lamellae secrete the anterior margin of the outer wall of the shell (Plate LXXII, Figure 3, *ip*). The epithelial layer covering the living chamber begins to secrete the last septum some distance from the anterior margin.

With the exception of the epithelial layer, the shell sac lining the interior of the living chamber becomes detached from the underlying septum after sectioning. The connective tissue of this part of the shell sac consists of fibrous elements and has a normal structure. There was a finely granulate clot between this layer and the sheath of the liver; the liver passes into the shell sac at the margin of the shell.

The part of the shell sac that is situated like a plug at the opening of the last siphonal neck into the living chamber and forms the transition to the siphuncle (Figure 4) is of particular interest. This part of the shell sac is swollen by ampulla-like dilatations of the vessels which belong mainly to the
435 venous stem. Into this swelling open larger vessels which later form thinner branches in the siphuncle. This "siphonal plug" is also characterized by a ring-shaped pad of connective tissue (Figure 4a) which is slightly thicker dorsally than ventrally and flattens gradually where it projects into the last siphonal neck. I considered this structure at first as a muscular pad; examination under high magnification, however, did not show muscle fibers between the dense and intensely stained, rounded nuclei. The pad also passes continuously into the fibrous layer of connective tissue of the shell sac. The epithelium of the shell sac which secretes the septa consists of high, cylindrical elements (*ep.*) in the area of the "siphonal plug". They again become flattened in the area of the 1st siphonal neck. This epithelial layer obviously secretes the siphonal neck. I can give no information on the assumed connection of this epithelial lamella and the siphonal epithelium, because the "siphonal plug" was torn off during preparation for sectioning and its connection with the siphuncle was loosened. On the other hand, the connection between the two epithelial lamellae could be proved with all desirable clarity in the larva, the siphuncle of which will be described in detail (Plate LXXIII, Figure 1). The siphonal necks, which form a funnel-shaped lengthening of the septa, too consists of very fine concentric chitinous lamellae which become easily separated during sectioning.

Siphuncle

The siphuncle is a direct continuation of the shell sac which lines the living chamber, but it differs from it in some aspects. The siphuncle is situated so loosely in the siphonal necks that it can be pulled out for some distance if the shell is opened. Examination of the siphuncle in alcohol without staining shows that it forms a cord which is slightly swollen at the transition of the septa into the siphonal necks and has a darker layer on the outside. This is followed by a light-colored layer which includes a fibrous axial tissue. The sections show (Plate LXXIII, Figures 2, 3) that the peripheral layer is the epithelium (*ep. s*), the light-colored layer consists of gelatinous connective tissue (*ga*), and the fibrous axial cord is formed by the capillaries of the siphuncle (*art.*, *v*) and with fibers of connective tissue between them.

The epithelium of the siphuncle is a direct continuation of the epithelium of the shell sac but its structure differs markedly from it. The epithelium consists of high cylindrical, partly cuboid elements from the end of the 1st siphonal neck. They are not continous but are separated by frequent intervals and often assume an irregular form or are curved. The epithelial layer is porous or spongy, with irregular invaginations, as shown in cross sections. The boundaries between the epithelial cells are often indistinct, especially at points of contact with the finely granulate, weakly staining plasma.
436 Such a point is shown in Figure 3, where the epithelium still adheres partly to the lamella. The boundaries of the cells are more distinct only in areas where the epithelial lamella is thicker and more strongly vacuolized. The nuclei stain intensively and have an irregular form; they are rarely rounded, usually oval or sinuate and sausage-shaped. That the epithelium of the siphuncle secretes the irregularly calcified pillar substance of the walls of the siphuncle that fills the space between the siphonal necks is shown not only by the position of the epithelium with respect to the siphonal necks but also by its structural resemblance to the epithelium of the siphuncle in *Sepia*, the structure of which is similar.

The light-colored layer of gelatinous connective tissue is situated below the epithelium. At some points (Figure 3, *ga*) this tissue appears as a delicate network which encloses the gelatinous substance and contains spherical or oval nuclei.

The axial tissue of the siphuncle is a modified continuation of the wall of the shell sac. Its basis consists of delicate strands of connective tissue, between which the gelatinous substance is less well developed. The gelatinous substance contains scattered elongate capillaries (Figure 2), some of which originate in the ampulla-like swellings in the siphonal plug. The capillaries apparently extend alongside each other through the whole siphuncle, without anastomoses. The venous capillaries (*v*) are wider than the arterial ones (*art*) which often show fine layers of circular muscles. There are about 12–13 larger capillaries in a single cross section. The axial tissue contains numerous nuclei which belong to the connective tissue cords, to the walls of the capillaries, or to the blood corpuscles.

The width of the siphuncle decreases toward the initial chamber, into which it projects (Plate LXXII, Figure 1). The siphuncle differs distinctly from the adjacent shell sac in that its tissue undergoes gelatinous degeneration in the juvenile chambers. This degeneration affects at first the epithelium and the connective tissue but later extends also to the vessels; single nuclei persist longest, but toward the first-formed chambers, they, too, disappear. The degeneration suggests that the siphuncle of the earlier chambers has lost its function and provides no further material for the formation of its walls.

The above details concern mainly the structure of the shell sac and the siphuncle; the shell of *Spirula* will be described together with the shells of other Cephalopoda by my pupil Stich. Moreover, Appellöf's excellent study of the shells of *Nautilus*, *Sepia* and *Spirula* is so detailed that the above data are only complementary.

5. Structure of the posterior end of the body

(Plate LXX, Figures 5–14)

The first description and illustration of a *Spirula* was given by Péron. The posterior end of this specimen was torn off, so that the shell was exposed. Animals with an intact posterior end were found
437 by Robert in 1836 on the surface between the Canaries and Cape Blanco, together with some damaged specimens. They were described in 1837 by Blainville, who confirmed Robert's statement that *Spirula* has two fins and a knoblike posterior end which covers the shell. Blainville therefore concluded that the shell is internal and covered dorsally and ventrally by the thin mantle, which forms the

so-called "bouton terminal". Later observers who examined the soft parts of *Spirula* described the terminal knob in detail and attempted to explain its function. Huxley, Pelseneer and Lönnberg studied sections of the terminal knob. Their conclusions are to some extent contradictory and present a rather incomplete picture of the structure of the terminal knob. This applies especially to the detailed description of Lönnberg, which contains valuable data but does not give a satisfactory explanation because of the poor condition of the material.

The terminal knob adheres closely to the posterior margin of the shell and is slightly dorsally displaced. It consists of a large ring wall of muscular and connective tissue (Plate LXX, Figure 5) which continues posteriorly and toward the middle into slightly narrowed lips which surround a pit ("aboral fossa" of Owen); a conical terminal papilla (*l.*) projects in its center. As shown by Huxley, the terminal papilla consists of an inner layer (*refl.*) of thick fibers adhering to the shell, a lens-shaped central body (*phot.*), and a process (*l.*) which forms the conical apex of the papilla and is described by Lönnberg as a "gelatinous layer". There is also a blood sinus (*sin.*) (overlooked by all observers) which surrounds the conical apex and part of the lens-shaped body. The whole formation is covered with epithelium, parts of which have a glandular structure. On the inside, i.e., toward the shell, it adheres closely to the epithelium of the shell sac (*sacc.*), as already recognized by Lönnberg.

As the terminal papilla is situated loosely on the shell, it is easily removed by a circular incision and sections which show the whole disc are obviously most instructive. Preservation in formol and subsequent treatment in alcohol is best for the demonstration of fine details. I stained the sections with solutions of carmine, hemalum and iron hematoxylin, of which the last gave the best results. I proceed to describe the individual parts of the organ in their order.

The **ring wall** is 9 mm wide and 2.5 mm thick. A groove separates it from the mantle where the musculature projects like a cheek. The absence of this groove in the *Challenger* specimen that Huxley, Pelseneer and Lönnberg called *Spirula peronii* is apparently caused by the fact that the anterior part of the body was completely retracted into the mantle and exerted pressure on the posterior part, thereby obliterating the groove. I do not agree with Lönnberg, who considers *S. peronii* as a different
438 species because of the absence of this groove. The ring wall flattens slightly toward the lens-shaped central body and continues posteriorly and inward in a marginal groove, which was distinct in our specimen only in one half (Figure 5). It consists of all tissue layers which form the mantle: outer epithelium, subcutaneous connective tissue, and musculature.

The epithelium is as flat as the other epithelium of the mantle, but it becomes gradually glandular toward the posterior side of the swelling. The gland cells are cylindrical, they do not reach the basal membrane and have conical nuclei in the proximal part (Figure 10). The secretion is yellowish, homogeneous or vacuolized, and does not fill the entire cell. Young gland cells have a small nucleus which stains strongly. The nucleus of intermediate and older cells becomes much larger and finally fills the greater part of the cell. Spherical nuclei of the reserve cells are situated proximally near the basal membrane. Between the gland cells are supporting cells which widen outward and have long, oval nuclei.

The connective tissue is a continuation of the subcutaneous tissue of the body. Near the mantle it consists of undulate strands of fibrillae which stain strongly. In the area of the ring wall the connective tissue becomes slightly looser and forms a large pad with a thicker cord of fibrils which extend toward the marginal lips. The loose tissue becomes gelatinous in and around the lips and near the central lens-shaped body. It now forms a network of lamellae that generally extend parallel to the surface but are frequently anastomosed.

The peripheral layers are slightly looser than the thicker inner layers, which gradually become

fibrous. Rounded and oval nuclei are situated on the lamellae, but may also be found in the gelatinous substance. Blood from the sinus (*sin.*) infiltrates into the peripheral layers, and blood corpuscles are recognizable at some points. This is apparently the tissue which LÖNNBERG described as "hemichondroid tissue", assuming that it supports the marginal lips.

Chromatophores (*chr.*) are numerous in this loose connective tissue. They are situated in light-colored spaces filled with liquid which permit free movement. They do not differ from the chromatophores described above. They have a large oval nucleus situated in the pigmented body, and a colorless, honeycomb-like peripheral layer from which extend contractile fibers with a nucleus at the base. The chromatophores are situated close to the epithelium in the lateral parts of the ring wall, but those in the area of the large central pad of connective tissue are situated at a distance from the epithelium, sometimes even near the central body.

Pigment cells are also present, though they were sometimes overlooked. The pigment cells belong to the loose gelatinous subcutaneous tissue. They are of irregular form and have small, pale, rounded or oval nuclei that are surrounded by a granulate, yellowish pigment (Figure 14). The pigment forms
439 either a spherical or an oval mass adhering to the nucleus, or small, rounded flakes which, too, surround the nucleus.

The musculature (*mu.*) occupies about one third of the ring wall, mainly in the parts near the shell. It consists mainly of strong ring muscles between which fibers radiate in all directions. In cross section the muscle fibers show the usual conditions: a central, chromatin-rich nucleus and a circle of contractile fibrils.

Numerous capillaries and nerves are present in the whole pad; the nerves were first noted by LÖNNBERG. Preparations stained with iron hematoxylin show thicker nerves, which generally extend toward the periphery and divide there into thin branches, which are sometimes distinct in the vicinity of the chromatophores.

Terminal papilla. The ring wall surrounds the conical ventral papilla which consists of three layers, as illustrated by HUXLEY. Adjacent to the shell sac is a layer of thick fibers of connective tissue, extending parallel to the shell (Figure 5, *refl.*, Figure 13); elongate, intensively staining nuclei lie between the fibers. These bar-shaped fibers sometimes show an indistinct fine striation. They become slightly looser laterally, where they pass into the connective tissue of the ring wall. Larger blood vessels are present between them, especially near the central body.

The central body (*phot.*), described by HUXLEY as a lens-shaped body, is decidedly the most interesting formation in the terminal papilla. I avoid the term "lens-shaped body" because sections show that it consists of two parts resembling butterfly wings, which are broadly fused in the middle and form pointed lateral processes. The central body is not enveloped in a special capsule as described by HUXLEY but borders toward the shell sac directly on the connective tissue bars, laterally on the connective tissue and the blood sinus of the ring wall, and posteriorly on the conical body.

It is difficult to describe this peculiar structure briefly. It consists mainly of lamellae of connective tissue, stratified parallel to the shell sac (Figure 6). Between the lamellae is a light-colored homogeneous substance through which pass numerous oblique bridges of connective tissue so that it appears at some points reticulate (Figure 9). The tissue retains its character toward the margin, but it becomes looser and more reticulate. A distinct capsule is absent. The nuclei of this tissue are pale, oblong oval, with coarser and finer chromatin granules (Figures 8, 9, *nu. phot.*); they are situated in the intermediate substance as well as near the lamellae, and are always arranged horizontally, i.e. in the direction of the lamellae.

440 Numerous capillaries are present in the central body; they branch mainly from larger vessels between

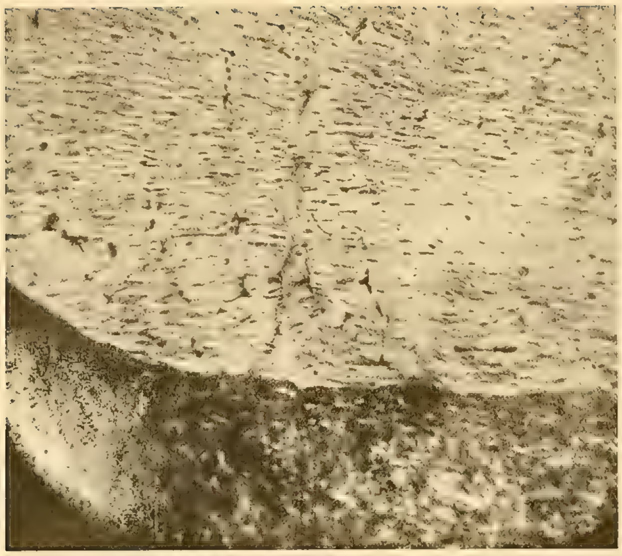

FIGURE 39. Part of luminous body (light-colored upper part) and of the cone of the lens (dark lower part). The luminous body contains nerves and capillaries.

the bars of connective tissue or from the lateral parts. The capillaries have a thin wall with elongate, strongly stained nuclei which usually appear tailed (Figure 3, *nu. cap.*). They contain rounded blood corpuscles, which are conglomerated at some points (*sang.*). They usually have two spherical nuclei which stain strongly, rarely a single nucleus; some nuclei are horseshoe-shaped and give the impression that they are about to divide. The capillaries are recognizable by their characteristic tailed nuclei, even when their walls are not distinct.

The central body also contains numerous **nerves.** LÖNNBERG overlooked the nerves because of the poor condition of his specimen. They usually have a thicker base and extend from the lateral walls, and especially from the surface facing the conical body (*l.*). If several nerves are situated closely together, one gets the impression that the margin of the central body projects like an arcade. Characteristically, the larger nerves penetrate the central body perpendicular to the direction of the lamellae and end in finer branches, most of them extending in the same direction, sometimes obliquely or even

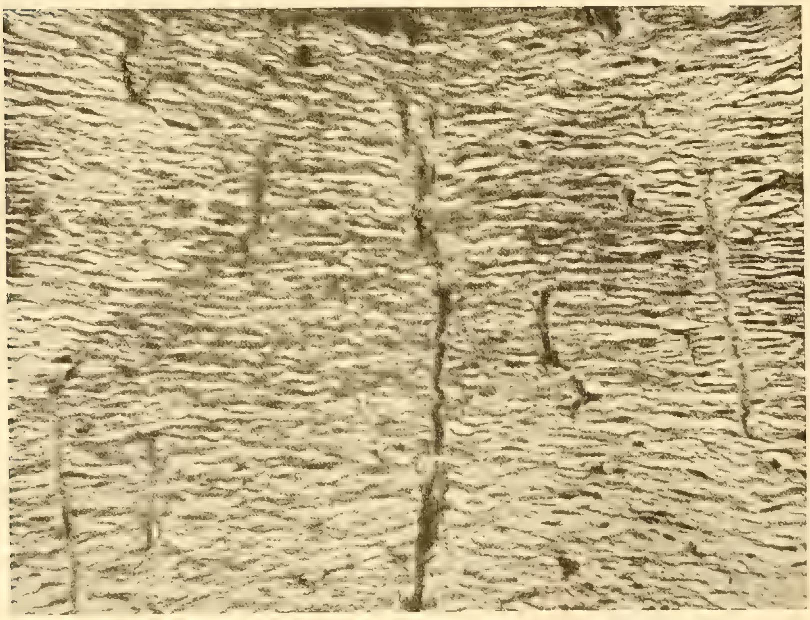

FIGURE 40. Part of luminous body, higher magnification. The horizontal lamellae are penetrated by vertical nerves; capillaries are visible for a short distance at some points.

441 horizontally (Figure 9). Some branches communicate with thicker stems (Figure 8). In preparations treated with iron hematoxylin, a few fibrils always stained intensively black (Figure 7, 8). In preparations not stained specifically, the nerve appears as a homogeneous gray cord and the fine branches are not visible. Near the nerve there are always strongly stained elongate nuclei, often of irregular form. These nuclei sometimes have lateral bulges; they are sometimes sickle-shaped or bent almost at a right angle, especially at the points where they radiate into the nerve (Figure 7). One is unable to make a section without cutting into the pale, radiating fibers amidst which elongate, often irregularly shaped nuclei always are found. Once one has attained familiarity with the tissue, it is not difficult to decide whether the nuclei belong to lamellae, capillaries, blood corpuscles or nerves, because this can be concluded from their form. LÖNNBERG recognized the different forms of the nuclei but provided no information on their nature. Only once he mentioned that the nuclei are connected with a fine fiber, which he tentatively considered to be a nerve.

The centrally situated apex of the terminal knob projects like a cone (Figure 5, *l.*); it consists of compact, vacuolated connective tissue which forms a network of dense anastomosing fibers with numerous nuclei of irregular form, at least in the central part (Figure 12). Toward the base and lateral parts of the central body, the tissue becomes reticulate, with smaller and larger meshes (Figure 11). The tissue is penetrated by thicker nerves which extend into the central body.

This conical process is surrounded by a large blood sinus (*sin.*), which contains blood corpuscles, often in large masses. Large slits filled with blood penetrate into the empty spaces in the conical process and apparently then unite into vessels. The blood sinus washes also the outward-facing lateral side
442 of the central body, and infiltrates from here into adjacent connective tissue of the ring wall. The blood sinus is bordered on the outside by the outer skin and the epithelium is not glandular and the cutis is very thin in this area.

Function of the terminal knob

No other organ of Cephalopoda has aroused so much controversy on its function as has the terminal knob. Its interpretation as an adhesive apparatus persists with striking tenacity to the latest

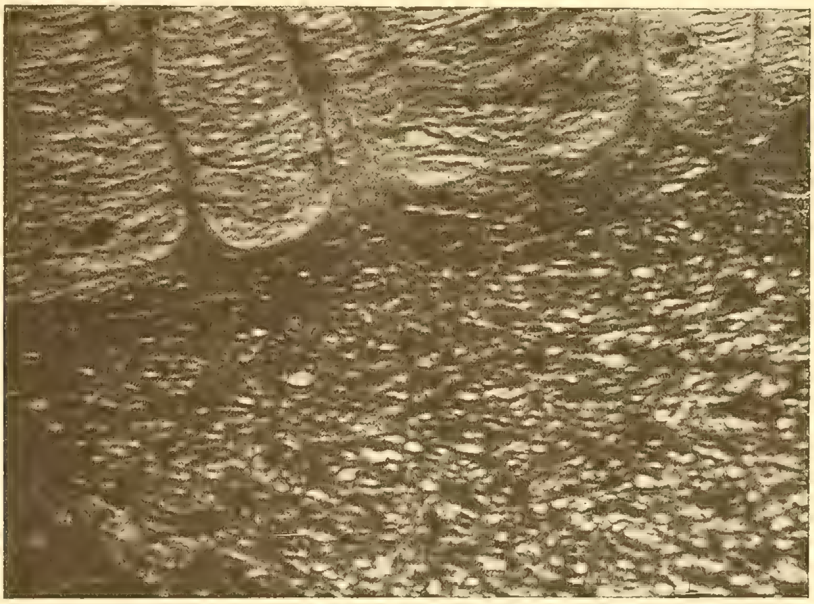

FIGURE 41. Boundary between luminous body (above) and cone of lens (below) with nerves penetrating in the form of an arcade.

publication on *Spirula*. It is certainly caused by a misunderstanding of a statement of RUMPHIUS, who gave the first description of *Spirula* in the "AMBOIN*schen Rareteit-Kammer*". It is appropriate that I repeat his presentation according to the German translation of MÜLLER and CHEMNITZ (Vienna, 1766, p. 18). RUMPHIUS states the following on *Cornu ammonis* (the shell of which is well illustrated on Plate XX, No. 1) in chapter 4:

> "The foremost chamber of the little post horns [ram's horns] is inhabited by a slimy animal which is firmly attached to a cliff by a thin spine which passes through the animal and through the opening of the first chamber. When a north wind causes an irregular motion of the sea, the post horns are torn from the cliff. This explains why they are always broken at the mouth. The pointed spines, however, remain firmly attached to the cliff; they are so hard that treading upon them wounds the feet."

This description shows that RUMPHIUS had only a vague idea of the soft body of *Spirula*, but he saw nothing which suggests a terminal knob. Contrary to the erroneous assumption of later authors, RUMPHIUS' data give no indication that the terminal knob serves for attachment. In fact, he considered the calcified siphonal necks as the apparatus for attachment. A similarity with other formations on coral reefs perhaps induced him to assume that the pointed spines remain attached to the cliffs after the other part of the shell has been broken.

The first exact description and illustration of *Spirula* was given by PÉRON and LAMARCK. However, the posterior end of their specimen was damaged and the shell was exposed. The first explanation of the significance of the terminal knob was given only by GRAY (1845, p. 259), who described it briefly as "a large, round, rather thick gland with a circular central cavity".

This interpretation of the terminal knob as a glandular formation was accepted by OWEN in his first description of *Spirula* (1848, *Voy.* "*Samarang*", p. 14). He assumed that the secretion serves for the attachment of the egg clusters. After OWEN had observed the same organ in a male *Spirula*, he abandoned this view and he interpreted it as a sucker in his detailed description of *Spirula australis*
443 (1879, p. 3). He writes: "If the disk were applied to a flat surface and the central part were withdrawn from the level, a vacuum would be produced, which would convert the disk into a sucker." OWEN is referring to the data of RUMPHIUS and attributes a function to the terminal knob which persists with striking tenacity to this day; JOUBIN, in a recent publication on the juvenile *Spirula*, also repeats this and speaks of a "ventouse impaire"—an unpaired sucker.

Studies of sections of the terminal knob showed convincingly that it cannot possibly act as a sucker. The central cone lacks longitudinal or radial muscles the contraction of which would create a vacuum when the ring wall is pressed against a surface. PELSENEER (1895, p. 18) stressed this and attempted to show that the terminal knob is a "protective organ" which would cushion the impact against hard objects. He assumed a similar function for the rostrum (i.e. the elongate posterior end of the gladius) of the Belemnitidae.

LÖNNBERG objected with justification to this interpretation. He stressed the presence of nerves in the ring wall and concludes that this organ is a receptor for hydrostatic pressure. I disagree also with this view, because there is no provision whereby changes in the pressure of the air enclosed in the chambers of the shell can be transmitted to a hydrostatic sense organ. The chambers are calcified, the siphuncle is surrounded by a completely closed, calcified siphonal neck and there are therefore no elastic walls as in the swimming bladder of pneumatophore of deep-sea siphonophores. It seems impossible that *Spirula* should be able to move vertically by compression of the air enclosed in the chambers. The only observation that would favor this assumption was given by GRAY, who reports in his description of *Spirula* (1845, p. 259) as follows:

"I am informed by M. Clausen that he had several specimens of this animal alive, and kept them for some time in 2 vessels filled with sea-water, and that they had the power of ascending and descending at pleasure."

This description gives no indication whether the vertical movement was caused by the ejection of water from the funnel, by movements of the fins, or by changes of the hydrostatic pressure.

I disagree with all these interpretations of the function of the terminal knob. It is not a gland, a sucker, a protective organ for the posterior end of the body, or a hydrostatic sense organ. What could be the function of an organ which is absent in the juvenile *Spirula* and appears late during postembryonic development? I know only one group of organs which develops at such a relatively late stage and which is an important character of deep-sea Cephalopoda, i.e. the luminous organs. **In my opinion, therefore,**
444 **the terminal knob is a luminous organ.** This is not an attempt to find a way out of a difficult situation, because it is based on the histological data described above. The different parts of the terminal knob can be easily related to those of a luminous organ. This applies especially to the central body, which contains numerous capillaries and perpendicular nerves that resemble those in the luminous organs of the Oegopsida. I regard this indeed as the **luminous body**, which emits light. The striated structure situated behind the luminous body and bordering on the shell or on the epithelium of the shell sac is the **reflector**, and the conical process which projects outward has to be considered as the **lens**. The ring wall which surrounds the organ not only serves for protection but also has another important function. The pressure exerted by the ring muscles at the base of the ring wall pushes the blood sinus, which is situated before the cone, outward, so that the cone becomes rounded like a lens. Although there is no pigmented envelope in the organ, it should be realized that it is situated directly on the opaque calcareous shell and is therefore as favorably situated as those luminous organs described which do not have a pigmented envelope.

This interpretation of the terminal knob has at least the advantage that it could be confirmed by observation of the live animal, and I hope that the occasion for this will be had.

6. Intestinal tract

(Plate LXVIII)

The **buccal cone** with its surrounding membrane is displaced slightly dorsally, as pointed out by Owen (1879, Plate 1, Figure 5) and Lönnberg (p. 103), while Huxley and Pelseneer (p. 29) state that it is situated in the center of the circle of the arms. This dorsal displacement of the buccal cone is also the reason why the ring formed by the buccal membrane is wider ventrally than dorsally. The buccal membrane is smooth on the outside and shows only the concentric stripes caused by the circular muscles. In contrast to the Oegopsida, the buccal membrane lacks supports and therefore also the attachments of the arms. Its inner margin is rounded, without points. However, weakly developed buccal supports are present in forms which are related to *Spirula* in some respects. This is especially the case in *Rossia*, in which the inner margin of the buccal membrane shows 6 weak swellings. The dorsal and ventral buccal supports are fused and form weak knobs. The 1st and 2nd arms are attached dorsally, the 3rd and 4th arms ventrally. In *Spirula*, the inner side of the buccal membrane bears meandering epithelial swellings which generally have a concentric course and continue on the outer side of the cone which is surrounded by the buccal membrane.

445 The mouth is surrounded by two **lips**, the outer one of which was overlooked in the past. It is not surprising, therefore, that the inner lips have been wrongly interpreted. Huxley and Pelseneer con-

sider them as outer lips, while Owen correctly names them inner lips but confuses the buccal membrane with the outer lips.

The **inner lips** of *Spirula*—like those of all other decapods—are well developed, thick and fluted. They have deep grooves between the 30 or so longitudinal swellings. Longitudinal sections show that the inner lips are thickened into an oval anteriorly and are thin posteriorly. Their outer margin bears the outer lips. Both are covered with an epithelium which consists of cuboid cells. Such cells cover also the folds, which appear like villi in sections. The cells have spherical or oval nuclei and a striated plasma at the base. The cells become cylindrical toward the outer lips and are here supplemented by gland cells between which the other cells now become elongate supporting cells. This glandular cylindrical epithelium is very thick on the anterior outer side, from the base of the outer lips. The gland cells disappear toward the anterior margin of the inner lips and the cells become lower and form a thick cuticle which covers the whole inner surface. The oval nuclei contain numerous chromatin granules and are situated in the middle of the cells, which show a fine fibrous structure. The cuticle shows a fine concentric striation; at some points it is detached from the underlying cells, which bear small processes separated by membranes. It is difficult to decide whether these processes are connected with a molt of the skin or secrete material for the inner layers of the cuticle. The greater part of the inner lips consists of ring muscles which are absent only at the narrowed base. Between them penetrate strong longitudinal muscles which extend from the pharynx and branch like a tree into ever thinner fibers. The space between the muscles is filled by loose connective tissue which penetrates between the epithelial layers of the folds and forms thinner strands which support the outer lip. Vessels of varying size and small nerve branches are present in the connective tissue.

The **pharynx** appears in lateral view with a flat dorsal side, a convex ventral side and tapering posteriorly. It is surrounded by a muscular sheath which consists of 4 to 5 bands of longitudinal muscles on each side and also covers the buccal ganglia. Cross sections of the posterior part show that the salivary duct is situated ventrally, and the two branches of the cephalic aorta pass on the right and left side above the salivary duct. The cephalic vein extends dorsally above the beginning of the esophagus. The cephalic vein and its branches widen ventrally toward the buccal ganglia, so that they are sickle-shaped in cross section. I do not know whether the branches of the cephalic vein become contiguous and fused into a completely closed venous sinus which surrounds the beginning of the esophagus. However, it is certain that the sinus is contiguous with the two arches of the aorta on their dorsal side and perhaps also with the salivary duct.

The **jaws** (Plate LXVIII, Figure 7) do not differ from those of other Decapoda. The rostrum of
446 the upper jaw projects sharply and bears a small tooth-shaped process at the base. This process is dark-brown and easily distinguished from the lighter palatine lamella. The rostrum of the lower jaw is short and ends in moderately wide wings which are situated on the gular lamella.

I cannot give information on the radula. I macerated the anterior part of the pharynx in cold KOH, which unfortunately destroyed the teeth of the radula, so that only the slightly corroded conical lateral teeth remained.

The **esophagus** contains 9–10 projecting longitudinal folds behind the pharynx, including two ventral folds which are strong in the area of the pharynx and form the border of a deep groove. The epithelium consists of cuboid cells which also show a fibrous structure at the base. These cells secrete a thick cuticle and have spherical nuclei. Below the epithelium is loose connective tissue with oval nuclei, which penetrates into the folds together with blood vessels. Then follow bundles of longitudinal muscles which are enveloped by circular muscles.

Sections show that this structure persists also in the area of the posterior salivary gland. The

esophagus passes through the two lobes of the liver (Figure 4, *oes.*) obliquely ventrally to the posterior third of the organ and appears on its ventral side (Figure 5). The esophagus widens slightly toward the stomach.

The **stomach and caecum** are situated in the form of a feed bag on the convex dorsal part of the anterior margin of the shell (Figure 1). The acorn-shaped stomach is situated on the right side, the caecum with the pancreas located on it are enveloped in a thin membrane and are facing left (Plate LXVII, Figure 3). If the stomach is empty, it is only about half as large as the caecum; the two organs are connected by a wide transverse duct the length of which is apparently an adaptation to the position of the organs on the shell sac (Plate LXVIII, Figure 5). The stomach of our specimen is 4 mm long; the long sac which encloses the caecum and pancreas is 11 mm long and is filled with a whitish clot.

The **stomach** (*st.*), or "cardiac stomach" according to Huxley and Pelseneer, projects slightly toward the esophagus and has thick muscular walls with about 12 inner longitudinal folds which are covered with a thick cuticle and are slightly wrinkled in the posterior part (Figure 5, *st.*). The broad connecting duct which probably corresponds to the gastric sinus of many Oegopsida contains about 6 projecting longitudinal folds and communicates with the **caecum** (pyloric stomach) through a broad opening with a sickle-shaped fold. The caecum is kidney-shaped and contains about 10 larger sickle-shaped folds covered with longitudinal muscles which alternate with weaker folds. These so-called spiral folds converge toward two swellings which pass to the beginning of the mid-intestine opposite the opening of the sinus which connects the stomach with the caecum. The mid-intestine (*int.*) passes through the renal sac, then forms a slightly spiral loop to the left (Figures 1, 5) and finally reaches the
447 rectum (*rect.*), which is not sharply defined and contains large longitudinal swellings. To the left of the rectum is situated the small, pear-shaped ink sac (Figures 2, 5, *atr.*), which is only 2 mm long and opens with a short duct in front of the anus. A broad gastro-genital ligament (Figure 1, *lig. g. g.*) connects the median inner side of the posterior third of the stomach with the large, posteriorly situated ovary.

Salivary glands. Cross sections of the terminal part of the pharynx at its transition into the esophagus show a small part of the anterior salivary gland. Wülker (p. 43) named the small outer lobes of the anterior salivary gland "buccal gland". The median mass of the gland, situated inside the pharynx, could not be demonstrated. Its arrangement resembles that observed in *Rossia.*

The posterior salivary gland (Figure 8) is situated on the posterior side of the cranium, dorsal to the process of the liver (cf. longitudinal section of the larva, Plate LXXIII, Figure 1, *gl. sal. p.*). The gland is 4 mm wide and 2.5 mm high. It forms a negative of the surface of the cranium, with shallow depressions corresponding to the static capsules. The gland is undivided but has the form of a butterfly with two dorsal and two ventral wings. It has a deep dorsal groove, in which the salivary duct, the esophagus, and the cephalic aorta are situated (Plate LXVIII, Figure 8, *a. ceph.*, *oes.*, *d. saliv.*). The two pallial nerves pass between the two wings and form a groove on the ventral wings. The salivary duct leaves the gland as a single canal. Sections show that the duct is formed by the union of two ducts which receive larger and smaller ducts. The opening of the duct will be described in connection with the larva.

The **liver** (Figures 1, 2, 4, 5, *hep.*) is cylindrical and 11–12 mm long. Its anterior side borders on the posterior wall of the cranium and bears shallow depressions for the static capsules. The posterior side of the liver forms a sickle-shaped dome which fills the terminal chamber of the shell and shows a groove formed by the margin of the shell (*x.*). The lateral walls are slightly ridged and are enclosed, as noted above (p. 335), by the muscular capsule of the liver. The liver consists of two separate, smooth-walled parts which are contiguous in the middle so that there remains a passage for the esophagus and the cephalic aorta which pass obliquely between the two lobes of the liver (Figure 4). The

two hepatic ducts (Figure 2, *d. hep. pancr.*) originate in the lower third, on the median ventral margin of each lobe. They are thick, widen only slightly and surround the beginning of the mid-intestine; they widen where they open into the anterior side of the caecum, at the beginning of the spiral folds (Figure 5, *d. hep. pancr.*).

448 The hepatic ducts bear small, thin-walled **pancreatic follicles** in the area of the mid-intestine. They become gradually larger and form two large glands which cover the left and dorsal side of the caecum (facing away from the ovary) and project markedly beyond the caecum (Figure 2, 5, *pancr.*). These two glands form a cluster and their ducts unite on each side into about 3 larger ducts and finally into a wide main canal (Figure 6) which opens broadly on the left side into the ring formed by the united hepatic ducts. The caecum and pancreatic appendages are enclosed in a thin-walled sac on which blood vessels branch (Figure 2, *sacc.*). This sac is apparently completely closed; it adheres to the beginning of the mid-intestine (Figures 1, 4, *s. st. coec.*). Its origin could not be determined but may be clarified should a similar structure be found to exist in *Rossia* or *Sepiola*. The sac contained a whitish clot, like the one usually present in the renal sac; but no relation to that could be found.

I would like to add some details on earlier communications. The best general descriptions of the intestinal tract were given by Owen, Huxley and Pelseneer. Owen (*Voy.* "*Samarang*", *Moll.*, pp. 9, 10) described it correctly and mentioned the divided liver and its ducts which are covered with pancreatic follicles. However, his drawing (Plate IV, Figure 15) and data are inadequate and his later drawings and descriptions (1879) give much additional information, particularly on the relative size of stomach and caecum. He also stressed that the posterior end of the divided liver is situated in the last chamber of the shell. Owen noticed the anterior salivary glands and gave a good drawing of the single posterior gland, but he described two efferent ducts.

The shortcomings of the descriptions of Pelseneer and Huxley are mainly a result of the strong contraction of the anterior part of the body, which was completely retracted into the mantle cavity and pressed on the vegetative organs, so that the anterior part of the liver became flattened and the stomach and caecum became compressed toward the posterior. The description is more detailed than that of Owen, but the only new information is the proof that the caecum and the pancreatic appendages are enveloped by a thin "peritoneal membrane".

7. Nervous system and sense organs

(Plate LXIX)

The nervous system of *Spirula* has only been incompletely described. Owen (1879) mentions merely the cerebral and optic ganglion and the pallial and visceral nerves. The description by Huxley and Pelseneer is slightly more detailed but gives only incomplete information on the structure of the nervous system. We shall give a more detailed description of the nervous system and I will mention
449 here only that I dissected the right orbit to obtain more correct details on the structure of the central and peripheral systems. However, the small size of the object made it impossible to give the exact description which I would have liked to give.

Central nervous system

Lateral examination of the central nervous system (Figure 4) shows that the centers are situated close together, not connected by the relatively long commissures which the drawings of Huxley (Plate

V, Figures 3–4) would indicate. Only the ganglion brachiale is situated at some distance and connected by a broad commissure with the ganglion pedale. The supra- and infraesophageal ganglia are also situated far from the cerebral ganglion. This condition is not isolated in the Myopsida: it is present also in *Rossia* (Winkler, 1914).

The ganglion cerebrale (*g. cer.*) extends dorsoventrally and has a cap-shaped middle part, the vertical lobe, which descends steeply toward the sharply defined anterior frontal lobe.

The ganglion viscerale (*g. visc.*) is almost spherical and shows no distinct division into those two dorsal tubercles that are sometimes named pallial ganglion. It adheres closely to the posterior side of the ganglion cerebrale and is covered by the esophagus. The cartilaginous roof of the cranium is thin behind the visceral ganglion and borders on the posterior salivary gland.

The ganglion pedale (*g. ped.*) is oval and situated ventrally, so that in dorsal view it is covered by the other ganglia.

The **system of commissures** is barely visible because the 3 posterior ganglia are situated closely together, but an indistinct tract is visible between the visceral and pedal ganglia behind the optic nerve. A large "bridge commissure" is distinct between the ganglion brachiale and the ganglion pedale. On the other hand, the broad cerebro-brachial and the brachio-buccal (*c. brach.*) commissures, which extend from the pedal ganglion to the supraesophageal ganglion, are distinct. These commissures form an elongate triangle in lateral view together with the thinner, long cerebro-buccal commissure (*c. cer. b.*), which branches immediately after leaving the apex of the brain. The two buccal ganglia are connected by a broad commissure which surrounds the esophagus (Figure 6).

Buccal ganglia (Figures 5, 6). The upper buccal ganglion (*g. bucc. sup.*) forms a half-ring with two lateral swellings (Figure 5); the ganglion buccale inferius—unknown until now—consists of two halves which are contiguous in the middle but are distinctly separated.

Comparison of the central nervous system of *Spirula* with that of other dibranchiate Cephalopoda shows a certain resemblance to *Loligo*, the central nervous system of which was described by Chéron
450 (1866, p. 62, Plate V, Figure 50) and recently also by Williams (p. 69, Figure 15). Furthermore, there is a close resemblance to *Sepiola* the nervous system of which was superficially illustrated by Pelseneer (*Syst. nerv. centr. Cephalop.*, 1888, Plate XXXVII, Figure 4), and to *Rossia* which was studied in detail by Winkler (1914).

Peripheral nervous system

Nerves of the ganglion cerebrale

1. Nervus opticus

The optic nerve is short and oval in cross section. It extends to the flat, oval ganglion opticum; the g. opticum is 5 mm long and is situated on the posterior margin of the orbit from which it is separated by the ring-shaped white body and by loose connective tissue through which pass fibers of the optic nerve.

2. Nervus olfactorius (*n. olf.*)

The olfactory nerve branches from the ventral margin of the nervus opticus at the boundary of the ganglion cerebrale and the ganglion pedale.

3. Nervus ophthalmicus superior (*n. ophth. s.*)

This nerve originates on the lateral posterior surface of the ganglion cerebrale and ascends obliquely anteriorly.

4. Nervus postorbitalis (*n. po.*)

It originates on the posterior margin of the ganglion cerebrale immediately behind the nervus ophthalmicus superior, then branches, pervades the cranium and innervates the dorsal musculature of the neck.

Nerves of the ganglion pedale

1. Nervus infundibuli anterior (*n. inf.*)

The anterior funnel nerve is very large and originates on the posterior ventral side of the ganglion at the point where the vena cava leaves the brain. It forms thick branches of which the posterior one divides again into 4 branches.

2. Nervus staticus (*n. stat.*)

I prepared only one branch of this nerve; this branch is situated directly behind the funnel nerve and extends to the static capsule.

Nerves of the ganglion viscerale

1. Nervus visceralis (n. visc.)

This nerve is strongly developed and begins with two branches which are at first situated closely together but then diverge and are situated in shallow grooves of the cranium which adheres closely to the visceral ganglion at this point. The two visceral nerves pass in a curve over the median dorsal side of the static organs and then extend ventrally and accompany the vena cava. They form a short, wide commissure immediately in front of the renal papilla which was noted by Pelseneer, and then
451 branch into the branchial nerves which begin closely behind the papilla and extend toward the gills.

2. Nervus infundibuli posterior

It is the nerve which originates laterally to the visceral nerve and closely to it which I interpret as the posterior funnel nerve. A similar nerve was mentioned by Chéron in *Sepia* and by Williams in *Loligo*. Recent authors (Hillig, 1912, p. 777; Richter, 1913, p. 364; Winkler, 1914) describe it in detail in various Decapoda.

3. Nervus pallialis

The two very thick pallial nerves (observed already by Owen) originate on the dorsal posterior side of the visceral ganglion. The posterior salivary gland forms a groove around these large nerves on each side. From the base of the pallial nerve branches a thin nerve (*n. coll.*) which innervates the adjacent parts of the collaris; I consider this nerve as homologous to the nervus collaris of recent authors. After passing through the sheath of the musculus retractor capitis, the pallial nerve (Figure 1, *n. pall.*) extends to the ganglion stellatum (*g. st.*) without a lateral branch. The two ganglia stellata are surrounded by loose connective tissue which Huxley (Plate V, Figure 6) names venous sinus. These ganglia are not oblong but broadly conical and send off four large nerves on each side. The preparation of the right ganglion shows also four smaller nerves one of which passes along the main stem (*n. pinn.*) toward the fins but is not united with it. Pelseneer proved that the two ganglia stellata are connected by a commissure (p. 36, Figure N), from which extends a thin median nerve. I prepared only the beginning of this commissure.

It should be stressed that the ganglion stellatum is embedded in the main stem of the pallial nerve which continues as the nervus pinnarum along the shell sac. Like HUXLEY and PELSENEER, I did not find a separation of the ganglion stellatum from the main stem with which it is connected in other Decapoda by a triangle of commissures, namely the inner and outer pallial nerves.

The n. pallialis externus and internus divide near the ganglion stellatum. These two branches are situated so closely together that only a narrow longitudinal slit shows the division between them (Figure 1). This condition resembles that in *Illex* (RICHTER, p. 351), although it is present also in the Myopsida. According to APPELLÖF (1898, pp. 588, 601), this slit is short in *Sepiola* and *Idiosepius* and apparently absent in *Sepiadarium*. However, APPELLÖF's illustration (Plate XXXIV, Figure 27) does not agree with the text, as it shows a slit on the distal part of the n. pallialis. Such a slit should be expected in the proximal part. I think, therefore, that this is probably a mistake and that the condition of *Sepiadarum* resembles that in *Spirula*.

4. Nervus retractor capitis anterior (Figure 4, *n. retr. cap. a.*)

I consider the nerve which originates behind the nervus collaris, passes through the capsule of the cranium and branches in the dorsal musculature as homologous to that described by HILLIG (p. 776) as the nervus retractor capitis anterior.

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Nerves of the ganglion brachiale

The nerves originating from the ganglion brachiale are more numerous than described in the past.

1. Nervi brachiales

There are 5 such nerves on each side. The 4th nerve, the nervus tentacularis (*n. tent.*), innervates the tentacles; the others enter the arms and are connected only by a simple commissure in the 2nd and 3rd arms. A common root of the nerve of the tentacle and the nerve of the arms is apparently absent, in contrast to the condition in *Chiroteuthis*.

2. Nervi antorbitales superiores (*n. a. o. s.*)

These nerves originate—from a common root which branches into at least 3 larger branches—behind the nerve of the 1st arm and extend into the dorsal musculature of the orbit.

3. Nervi antorbitalis inferiores (*n. a. o. inf.*)

These 3 thick nerves innervate the ventral musculature of the orbit. The two anterior nerves are situated close to the last nerve of the arm. HILLIG (p. 785) recently described the anterior of these nerves as "nervus ophthalmicus inferior anterior" (*opht. inf. a.*).

Nerves of the ganglion buccale superius

1. Nervi suprapharyngei

There are 3 such nerves, one of which leaves at the beginning of the commissure and curves ventrally. They innervate the dorsal and lateral musculature of the pharynx. HILLIG named them "nervi labiales" because they enter the lips.

Nerves of the ganglion buccale inferius

1. Nervi infrapharyngei

These are two large nerves which branch soon after their exit and innervate the lateral and ventral musculature of the pharynx. Hillig named them "nervus mandibularis" and "nervus maxillaris".

2. Nervus sympathicus

I observed the root of this nerve only on one side. It apparently extends along the esophagus to the ganglion gastricum which is situated in the corner between the esophagus and the sinus that connects stomach and caecum (Plate LXVIII, Figure 5, *g. gastr.*). Branches of this nerve extend to the stomach, caecum, mid-intestine and to the hepatic ducts.

Eye

(Plate LXIX, Figures 1, 2, 3)

The form of the eye has been described above (p. 326).

453 The relatively thin-walled **eyeball** is strengthened by a broad cartilaginous girdle (Figure 3, *cart.*) which leaves the fundus free and ends not far from the epithelial body. The cartilage becomes a thin hyaline lamella without cellular elements on the posterior side. The cartilage is covered on the outside with a delicate muscular lamella which consists of circular fibers. This lamella is not very thick and is thinnest near the cartilaginous ring. The cartilage and the hyaline lamella are covered with a thin layer of connective tissue that becomes thicker, loose and well vacuolized between the epithelial body and the anterior margin of the retina.

The **epithelial (ciliary) body** is very thin compared to the thick lens and is scarcely thicker than the adjacent wall of the eyeball (Figure 2, *c. cil.*). The half facing the vitreous body contains a blackish pigment, the opposite half lacks pigment, so that the groups of epithelial cells are distinct in sections. Langer's muscle, which is inserted on the outer margin of the cartilage, is only moderately developed; it consists mainly of radial fibers and a few circular fibers.

The **iris** (*ir.*) passes into the eyeball at the beginning of the epithelial body and at the insertion of Langer's muscle. It has a pigmented inner surface. The marginal circular fibers begin only at the level of the surfaces dividing between the two halves of the lens; they gradually thicken toward the margin of the iris. The cross section of the ring of vessels is visible some distance from the base of the iris.

The **retina** (*ret.*) occupies about two thirds of the eyeball and flattens anteriorly some distance from the epithelial body. This anterior margin of the retina is visible, even from the outside, as a whitish stripe. Except for its margin, the retina is uniformly thick and shows neither a fovea nor the stripes observed in surface forms. Between the retina and the eyeball or cartilaginous ring there is a layer of nerve fibers which originate as thick, branching bundles from the ganglion opticum (*g. opt.*). The white body (*c. alb.*) and the loose connective tissue separate the optic ganglion from the eyeball.

The different layers of the retina (Figure 3) are composed as follows. The layer of sensory cells (*s.*) has small spherical nuclei, stacked upon each other 8–10-deep in the middle of the retina. Between this layer and the rods (*st.*) is a pigmented layer (*pg.*) which is 0.02 mm thick. This is the typical condition of dark adaptation, i.e., the layer of rods is completely free of pigment.

There is no distinct difference in the thickness of the rods. They are about 0.13–0.14 mm long in the center and become shorter toward the periphery. A membrana limitans forms the boundary toward the vitreous body.

Static organ

I have only determined the number of cartilaginous processes, of which there are 8 on the right organ. The statolith, which is situated at the bottom of the organ at the boundary between the visceral and the pedal ganglion, has an almost golden sheen. It is of characteristic form: laterally compressed,
454 with the narrow edge situated on the crista acustica. Its broad side is more or less rhomboidal, with a spherical thickening at one corner. From the narrow side it resembles a hammer with a curved handle and a spherical head (Plate LXIX, Figure 7).

8. Vascular system

(Plate LXX, Figures 1–3)

The vascular system is only incompletely known. OWEN described the heart, branchial heart and some larger vessels, but without indicating exact data. More detailed descriptions were published by HUXLEY and PELSENEER; these, however, contain some errors which should be corrected as these points are important for the determination of the systematic position of *Spirula*.

The vena cava (Figure , *v. c.*) is not visible on the abdominal integument as it is covered by the muscular capsule of the liver. It receives the two hepatic veins (*v. hep.*) from the liver which open at the level of the renal papillae. It then divides into its two main branches which are covered with venous appendages and are not fused into an unpaired median mass. They extend to the point where the branches of the vena cava open into the branchial heart. The two complexes of venous appendages later receive the abdominal veins (*v. abd.*), which pass on both sides of the shell sac and receive a number of small veins from it. The pallial veins (*v. pall.*) open into it on both sides. The left pallial vein receives some large veins which accompany the oviduct (*v. od.*) and the oviduct glands.

The pallial veins form 3 branches to the mantle; the middle branch extends directly to the mantle, the other two—the rami anteriores and posteriores—accompany the pallial nerves. The ramus anterior passes ventrally behind the ganglion stellatum and branches further from there.

The vena genitalis also opens into the complex of venous appendages. As the ovary is mature, this vein is large, passes near the genital artery in the gastro-genital ligament (Plate LXVIII, Figure 1, *lig. g. g.*) and has here a spindle-shaped swelling. HUXLEY (Plate VI, Figure 3, *Z*) considered this as a gland situated on the stomach, without recognizing its connection with the genital vein. I made cross sections of this formation to determine its function and found that it is a blood gland, formed by fine ramifications of the genital vein. The genital vein divides into lateral branches which look in cross section like a tree and are covered with a single layer of epithelial cells (Plate LXX, Figure 4). I do not know the function of this gland.

The branchial hearts (*c. branch.*) are oval and have rounded posterior appendages (Plate LXVII, Figure 2, *app.*) which end in a few villi. The branchial arteries, which originate from the branchial hearts, extend ventral to the mantle veins; the branchial veins (*v. branch.*) are situated between the mantle veins and the branchial arteries and widen only slightly at their opening in the heart.

455 The **heart** borders posteriorly on the shell sac and is covered laterally by the venous appendages and ventrally by the beginning of the mid-intestine. The large right lobe of the ovary extends to the heart. The heart is spindle-shaped and markedly widened between the openings of the branchial veins. At its anterior margin, slightly to the right, originates the cephalic aorta (*a. ceph.*) with a broad base; it then becomes narrower, and again forms a slightly spindle-shaped swelling and extends dorsal to

the esophagus. The cephalic aorta branches into the gastric artery (*a. gastr.*) in the area of the second swelling, and sends off branches to the stomach and pancreas. The hepatic artery branches from it in about the lower third of the liver (Plate LXVIII, Figure 4). The posterior aorta (Plate LXX, Figure 1, 2, *a. post.*) originates at the posterior margin of the heart, slightly ventral, obliquely opposite the cephalic artery and in about the middle of the heart. The posterior aorta, or abdominal artery, branches into the recurrent artery near its base, which then branches and supplies the left and right renal sac (*a. n.*) and ink sac (*atr.*); it has a large branch on the left toward the stomach and intestine (*a. g.*). Another branch extends along the posterior margin of the left renal sac toward the branchial heart. The stem of the posterior aorta extends along the right wall of the shell sac, with a branch along the renal sac to the right branchial heart and then with another branch to the left for the shell sac (*a. sacc.*).

The genital artery (Figure 1, *a. gen.*) originates on the dorsal side of the heart opposite the posterior aorta, continues along the gastro-genital ligament and together with the genital vein extends to the ovary where it branches.

The presence of an independent genital artery is of interest because Brock (1880, p. 64) and Appellöf (*Jap. Ceph.*, 1886) state that it has an independent origin only in the Myopsida. Pelseneer overlooked the genital artery of *Spirula* and considered the recurrent artery as the genital artery. According to Brock and Appellöf (*Chaunoteuthis*, Plate III, Figure 16), an anterior artery originating directly from the heart is absent in *Spirula* and is apparently replaced by the recurrent artery. Nor does Williams (1909, p. 57) mention an independent anterior artery in *Loligo*. The branches to the ink sac, renal sac, rectum and branchial hearts mentioned by Williams probably belong to the area of the recurrent artery.

9. Renal sac

Opening of the mantle cavity shows the two chimney-shaped renal papillae (Plate LXVII, Figur 2, *ur.*) near the anus. The position and form of the papillae resemble those of the Dibranchiata. They are flattened in the *Challenger* specimen because of the strong contraction of the anterior part of the body, which affected all soft parts. The illustration of the specimen of the *Blake* by Agassiz (reproduced by Huxley on Plate II) shows chimney-shaped renal papillae near the anus, too, just as does our specimen.

That the presence of 2 renal papillae does not indicate a complete division of the renal sac is
456 proved by the condition in the Oegopsida and the well-described Myopsida. Pelseneer states that there are two separate renal sacs in *Spirula* and illustrates this (Figure S, p. 38). I decidedly disagree. Removal of the abdominal wall shows that the two sacs communicate broadly behind the mid-intestine and anterior to the shell sac (Plate LXVII, Figure 2, *nephr.*) and a similar condition is present anterior to the intestine. This is thus a single renal sac, which is traversed by the mid-intestine and which from the papillae posteriorly widens like a funnel. The posterior margin of the renal sac borders in the middle on the shell sac, on the right on the ovary and on the left on the thin sac which envelops the caecum and pancreas. The renal sac is bordered laterally by the branchial hearts and the oviduct and dorsally by the heart with the cephalic aorta and the venous appendages of the vena cava. It is covered centrally by the thin abdominal wall and the rectum.

This description of the renal sac suggests a comparison of its form in the Oegopsida and Myopsida. The mid-intestine of the Oegopsida never passes through the renal sac but anterior to it, whereas in the Myopsida the mid-intestine passes through the middle of the renal sac and divides it into an anterior

and a posterior part which broadly communicate. This condition has been described by Grobben and Vigelius in *Sepia* and other Myopsida; it also applies to *Spirula.*

I am not sure whether the renal sac of *Spirula* forms a dorsal evagination as that described for *Sepia* and *Loligo.*

10. Genital organs

The specimen is a mature female. The position of the ovary does not differ from that of other mature females dissected. The ovary fills the entire posterior part of the body (Plate LXVII, Figure 2) and forms a large right lobe (*ov.*) which is connected dorsally with a smaller left lobe (*ov.'*). The ovary is 12 mm long and 14 mm wide. It borders dorsally and laterally on the shell sac. It reaches the branchial heart, renal sac and stomach on the right, and penetrates on the left into the body cavity between the caecum and shell sac. A broad, short gastro-genital ligament (Plate LXVIII, Figure 1, *lig. g. g.*), on which the genital artery and vein are situated, attaches the ovary to the inner side of the stomach. The easily separated eggs are in different stages of development; they measure 1.7 mm in diameter when mature.

The **oviduct** (Plate LXVII, Figure 2, *ovd.*) is unpaired and situated on the left side, in contrast to the Oegopsida which always have paired oviducts. I found only in *Pterygioteuthis* that the left oviduct was reduced so that only the right oviduct was present, in contrast to *Spirula.* The oviduct
457 of *Spirula* is situated ventrally its whole length; it is covered by the two left nidamental glands and opens near the left renal papilla. The oviduct extends obliquely to the base of the left gill, which covers it ventrally together with the branchial heart and the large branchial vessels. The oviduct then forms a whitish formation (*od.'*), visible on the left side of the abdominal wall, and extends to the level of the left ovary. The oviduct consists of adjacent arms which are posteriorly fused in a loop (Plate LXX, Figure 1). The recurved arm which faces the middle is slightly longer than the other, which is directed anteriorly; the longer arm contained about 20 eggs. The recurved beginning of the oviduct has a slit-shaped opening (*or. od.*) in the body cavity, i.e. in the coelomic chamber for the right branchial heart, at about the level of the ring system of the oviduct gland. This arm was transversely wrinkled, as it contained no eggs.

The oviduct gland is flask-shaped and 8 mm long. Its ring system is well developed as in *Sepiola*, while the fork system is not markedly swollen and resembles a slender bottleneck. The spermatophore sac which is present in front of the opening of the oviduct in *Sepiola* and some species of *Rossia* is absent.

Comparison of previous publications with the above data shows that Owen, Huxley and Pelseneer overlooked the two-armed form of the oviduct and did not notice that such a condition is apparent in *Sepiola* and *Rossia* (Döring, 1908, Figures 13 and 16). The oviduct of the above two genera is also curved anteriorly but not as far as in *Spirula.* The oviduct of *Sepiola* and *Rossia* begins with a short recurved arm which curves into a much longer arm. A condition resembling that in *Spirula* may be found in other Myopsida, e.g. in *Idiosepius*, according to the illustration of Appellöf (1898, *Ceph. von Ternate*, Plate XXXII, Figure 3). However, it is certain that this is the final stage of the development of the oviduct which leads from the terminal ampulla of the Oegopsida to *Rossia* and *Sepiola* and finally to *Spirula.*

The **nidamental glands** consist of the nidamental and the accessory nidamental glands (Plate LXV, Figures 1, 2; Plate LXVI, Figures 3, 4). They are not contiguous in the median line as in *Rossia* and

Sepiola but widely separated by the shell sac which extends to about their posterior third. The nidamental glands are 6 mm long and 4 mm wide, oval, and show a uniform development of the two series of lamellae with a large semicircular base. The accessory nidamental glands are separated as in *Rossia* and *Loligo*, relatively large, 5 mm long and wide. They form two diverging arms and border anteriorly on the dorsal side of the nidamental glands. Like all the Myopsida, they have no regularly arranged systems of lamellae, a condition already observed by PELSENEER. According to APPELLÖF, the accessory nidamental glands of *Spirula* resemble those of *Idiosepius*.

OWEN (1879, p. 12) mentions only one pair of nidamental glands, apparently the accessory glands,
458 but HUXLEY and PELSENEER mention both pairs. The nidamental glands are correctly illustrated by AGASSIZ, who gives a better picture of the mantle complex than HUXLEY.

Attachment of the spermatophores

As noted above, there is no spermatophores sac in front of the oviduct of *Spirula*. This condition is explained by sections of the buccal lip. The preparations show strongly stained bundles the function of which I did not understand at first. Closer examination showed that these are spermatophores, which are deposited in *Spirula* between the grooves of the fluted inner buccal lip. I later found between the buccal lips a number of additional spermatophores which had already everted their tube. These spermatophores contained sperm enclosed in a thin membrane and a cap of a gelatinous, gluelike substance at the base. This is of interest because a similar condition was found by STEENSTRUP to be characteristic for the Loliginidae and Sepiidae. In his work on *Hemisepius*, STEENSTRUP (1875) developed the suggestions which he had indicated already in his first publication (1856) and also presented illustrations. Later (1881) he showed that the spermatophores are attached near the mouth also in the genera *Sepiadarum* and *Idiosepius*. However, all the forms examined differ from *Spirula* in that their spermatophores are attached on the inner side of the buccal membrane and not between the grooves of the inner buccal lips. Except for this topographical difference, which I do not consider important, the condition in *Spirula* is of interest for the determination of the systematic position of this genus because it closely resembles that of some Myopsida but does not occur at all in the Oegopsida.

11. Systematic position of *Spirula*

A discussion of the systematic position of *Spirula* is necessary because there is still no agreement whether this genus belongs to the Oegopsida or the Myopsida. The early authors stressed the relationship of *Spirula* to fossil forms and considered it as a representative of the family Spirulidae which contains the last surviving descendant of fossil forms like *Spirulirostra* and *Beloptera*. OWEN (*Trans. Zool. Soc.*, 1836), who established the family Spirulidae, speaks on this subject less decisively than D'ORBIGNY (*Moll. vivants et fossiles*) and GRAY (*Catal. Moll.*, 1849, p. 113). Both authors placed *Spirula* (*lituus*), *Spirulirostra* and *Beloptera* in this family; GRAY changed its name to Litulidae.

The question whether *Spirula* belongs to the Oegopsida or to the Myopsida was first discussed by STEENSTRUP, who stressed the myopsid characters of this genus. In his work on *Sepiadarium* and
459 *Idiosepius*, STEENSTRUP (1881) stressed the close relationship between *Spirula* and *Idiosepius* and placed the two genera in the group Idiosepii, thereby placing *Spirula* in his family "Sepio-Loliginei". STEENSTRUP based his view on the type of hectocotylization, the systematic value of which he defined most sharply in his work *Notae Teuthologicae* (1887, p. 67):

"Hectocotylatio bene observata et rite considerata divisionibus naturae semper congruit, incongrua divisionibus, eas arbitrarias et factitias esse indicat."

Spirula has two hectocotylized ventral arms, as proved first by Owen (*Proc. Zool. Soc.*, 1880, p. 352) and later confirmed by Steenstrup. The hectocotylized arms are longer than the other arms, which are very short; they have 4 sides, bear no suckers and the right hectocotylus is much longer than the left one. *Idiosepius* is the only myopsid which shows a similar condition and also has two hectocotylized ventral arms that bear no suckers, and Steenstrup therefore placed the two genera in the same group.

We have today a different opinion of the systematic importance of the hectocotylization. It certainly has systematic importance, but the type of hectocotylization as defined by Appellöf, Brock and Vigelius has the same importance as any other morphological fact. However, the great scientist showed a correct systematic instinct when he placed *Spirula* in the Myopsida.

Pelseneer strongly objected to this and placed *Spirula* in the Oegopsida. In this he based himself mainly on the eyelids, the elongate form of the central nervous system, the close connection between the visceral nerves behind the anus, the well developed anterior salivary glands and the fact that the esophagus and aorta do not pass through the liver. As further characters of the Oegopsida he considered the origin of the genital artery on the posterior aorta, the sessile outer openings of the renal sac, and the incompletely retractile tentacles.

Lönnberg later disputed some of Pelseneer's data and defended the myopsid character of *Spirula*. However, this attempt attracted little attention because he did not dissect his specimen and gave only a few histological data. Appellöf (1898, p. 621) placed *Spirula* in the Oegopsida on the basis of the data of Pelseneer.

Hoyle (*Advanc. Sc.*, 1907, p. 7, Brit. Ass.) also disagreed with Lönnberg. He compared the structural conditions of *Spirula* with the Oegopsida and the Myopsida and concluded that this genus is intermediate between the two groups and may prove to be a representative of a separate suborder of the same rank as the other two. Hoyle thus accepted the views of Brock, who at first (1879) considered *Spirula* as a myopsid but later (1880) concluded that it probably belongs to a separate group which is intermediate between the Oegopsida and the Myopsida.

460 I shall now explain my concept of the systematic position of *Spirula* as presented before the Zoological Congress in Frankfurt (1909). In my opinion, *Spirula* belongs without doubt to the Myopsida. The decisive arguments put forward by Pelseneer in favor of the opposite view are based on wrong observations and interpretations. Let us therefore examine in detail the structures which demonstrate the relationship of *Spirula* to the Myopsida.

1. The **shell** of *Spirula* is isolated among the recent Cephalopoda and shows relationships with fossil forms, as the early authors recognized, but does not resemble the shells of the Oegopsida the gladius of which consists only of chitin. Only the Sepiidae have calcified shells and show some structural similarities with the shell of *Spirula*, as was primarily shown by Appellöf. Moreover, the shell of *Spirula* is not external, as described by Pelseneer, but situated inside the body, also in the adult. At the "ovals", where the shell appears to be external, it is actually covered with the extremely thin skin of the mantle. After Joubin had described a larva with a completely internal shell of only 6 chambers—and I was able to confirm this in larvae caught by the *Michael Sars* Expedition—there seems to be no doubt that this is an internal shell.

2. The **central nervous system** of *Spirula* does not have the elongate form and the long commissures between the centers described by Huxley and Pelseneer. The central nervous system of *Spirula* resembles most closely that of *Spirula* and *Rossia*.

An argument for the oegopsid nature of *Spirula* concerns the pallial nerve, which divides close to the stellate ganglion into an inner and an outer branch, though the former does not extend far. Such a condition has been demonstrated in *Illex*, but *Sepiola* shows similar conditions, too.

Pelseneer considers the short commissure between the two visceral nerves as a character of the Oegopsida but Lönnberg stated that the length of this commissure varies markedly in both groups. The recent studies of Hillig (1912) and Richter (1913) confirm this.

3. The **intestinal tract** shows a number of important characters that are completely absent in the Oegopsida. I was unfortunately unable to obtain an intact radula. However, according to the illustration of Oegopsida and Myopsida, the radulae should be expected least of all to provide a decisive answer. The number and form of the teeth vary so markedly that the radula of some Oegopsida resembles that of the Myopsida and the radula of some Myopsida resembles that of the Octopoda.

461 More important and decisive is the fact that the esophagus with the accompanying cephalic artery passes between the two parts of the liver and not on their dorsal side, as is the case in all Oegopsida.

The ratio of size of stomach and caecum cannot be used for determination of the systematic position, because it varies markedly both in the Oegopsida and the Myopsida, and often even within the same family. However, *Sepiadarium* and *Spirula* have a large kidney-shaped caecum and a smaller stomach, a condition which reaches its extreme in *Idiosepius*.

The salivary glands of *Spirula* closely resemble those of *Rossia* and *Sepiadarium*. The extrabulbar part of the anterior salivary glands is reduced, and the posterior glands are fused anf form a deep groove in which pass the esophagus and the aorta, as in *Rossia*.

The liver provides one of the main arguments that *Spirula* belongs to the Myopsida: it is divided, a condition observed only in the higher Myopsida, the Sepiidae. We have extensive information on the form of the liver in the Oegopsida, so that it seems unprecedented that a divided liver or a liver with 2 posterior processes through which pass the esophagus and the aorta could be present in this group.

4. The muscular capsule of the liver of *Spirula* is completely closed on the dorsal side and shows almost no division between the musculi retractores capitis lateralis and medianus. This condition does not occur in the Oegopsida but it is particularly characteristic for the Sepiidae.

The musculi depressores infundibuli of *Spirula* are broadly truncate posteriorly, and situated on the muscular capsule of the liver, while they are pointed and extend dorsally beyond the base of the gills in all Oegopsida.

5. The **vascular system** shows an important condition which is present only in the Myopsida. The genital artery originates independently from the heart and is not a branch of the posterior artery. Pelseneer overlooked the genital artery and wrongly considered a branch of the posterior artery as this.

6. The **renal sac** is typical for the Myopsida. It does not consist of two separate renal sacs, as wrongly stated by Pelseneer, but is a single organ traversed in the middle by the mid-intestine, a condition present only in the Myopsida.

Pelseneer described the renal papillae as sessile and considers this as a character of the Oegopsida. In fact, many Oegopsida have projecting, chimney-shaped renal papillae. On the other hand, markedly raised papillae are present also in *Spirula*. This is proved by the early descriptions of *Spirula*, especially that of the specimen of the *Blake* which was illustrated by Agassiz. The renal papillae of *Spirula*
462 are displaced to near the anus, a condition present only in some Sepiidae.

7. The female **genitalia** show an unmistakable character of the Myopsida: the single oviduct on the left side. All Oegopsida have paired oviducts; the only case of reduction of one oviduct, in *Pterygioteuthis*, concerns the left oviduct. Especially characteristic for *Spirula* is the horseshoe-shaped loop formed by the oviduct, so that its opening in the body cavity is displaced far anteriorly to the

level of the oviduct glands. Such a looping of the beginning of the oviduct does not exist in the Oegopsida but it is present in *Sepiola* and *Rossia*, although less marked.

Another important myopsid character of *Spirula* concerns the presence of separate accessory nidamental glands which are absent in the Oegopsida; in cases in which they have been described (*Chiroteuthis* and *Leachia*), I proved that this is a confusion with luminous organs or oviduct glands. I have also shown that the spermatophores of *Spirula* are attached between the grooves of the inner buccal lips. This is an indication—though a biological, not a morphological one—that *Spirula* belongs to the Myopsida, as only species of the latter group show a similar attachment of the spermatophores—similar, that is, not exactly on the inner buccal lips yet still in the area of the inner wall of the buccal membrane.

Finally, the presence of two hectocotylized ventral arms has been demonstrated so far in only one other genus, *Idiosepius*, as STEENSTRUP noted.

Spirula thus shows the following characters which are present exclusively in the Myopsida:

1. The inner shell is calcified and chambered.
2. The liver is divided and pervaded by the esophagus and the aorta.
3. The muscular envelope of the liver is completely closed and borders on the broadly truncate posterior end of the funnel depressor.
4. The renal sac is traversed by the mid-intestine.
5. The genital artery originates independently, directly from the heart.
6. An oviduct is present only on the left side.
7. Accessory nidamental glands are present.
8. The spermatophores are attached near the mouth.

There remains a single character of the Oegopsida: the structure of the lid membrane, which does not extend as a transparent cornea over the lens and does not have a small lateral opening.

Although it is from the structure of the lid fold that D'ORBIGNY derived the names Oegopsida and Myopsida, this character should not be overestimated. The Myopsida known until now are either
463 surface forms living close to the shore, or benthic forms some of which burrow in the sand or mud. The lid fold, which extends over the pupil, is a protective organ analogous to the spectacles of snakes. Such a lid fold is also present in deepwater Myopsida which live on the bottom and have been caught only by trawling. *Spirula* is a pelagic animal and does not need such a protective modification of the lid fold. This applies not only to *Spirula* but also to pelagic deepwater Octopoda (Bolitaenidae, Cirrhoteuthidae, etc.). *Spirula* is the only pelagic genus of deepwater Myopsida and it is therefore not surprising that its lid fold has remained in a state typical for pelagic Oegopsida.

As to relationships between *Spirula* and the different families of Myopsida, it appears that it shows similarities to all of them. However, these similarities do not justify the inclusion of *Spirula* in any of their families.

The relationships with the **Loliginidae** are shown by the following characters:

1. A free cartilaginous closing apparatus on the funnel and neck is always present.
2. The median and lateral adductors of the mantle are absent.
3. The posterior salivary glands are fused.
4. The accessory nidamental glands are separate and the spermatophores are attached to the buccal membrane.

With the **Sepiolidae** *Spirula* has the following characters in common:

1. The funnel adductors are not visible from the outside.
2. A free cartilaginous closing apparatus is present only in *Rossia* and *Semirossia*, while in the other genera of Sepiolidae there is a reduction of the neck cartilage, and in *Sepiadarium*, also a disappearance of the funnel cartilage.
3. The muscular capsule of the liver is completely closed.
4. The posterior salivary glands of *Sepiadarium*, *Rossia* and *Heteroteuthis* are fused; those of *Rossia* and *Spirula* are very similar.
5. The anterior salivary glands of *Spirula* resemble those of *Rossia* and *Sepiadarium* in the presence of an extrabulbar, but already reduced, part.
6. The oviduct of *Sepiola* and *Rossia* forms a recurved loop which is, however, much shorter than in *Spirula*.
7. *Rossia* and *Sepiadarium* have separate accessory nidamental glands.

Relationships with the **Idiosepiidae:**

1. There is resemblance in the form of the body caused by the short, rounded, subterminal fins.
2. A free cartilaginous closing apparatus is present.
3. The funnel adductors are not visible from the outside.
4. Both ventral arms are hectocotylized.
5. The muscular capsule of the liver is completely closed.

464 6. The caecum is larger than the stomach.

7. The anterior salivary glands are partly extrabulbar.
8. The accessory nidamental glands are separate and horseshoe-shaped, and closely resemble those of *Spirula*.
9. Spermatophores are deposited on the buccal membrane.

With the **Sepiidae** *Spirula* has the following characters in common:

1. An internal shell with calcareous septa.
2. A free cartilaginous closing apparatus.
3. The funnel adductors are not visible from the outside.
4. Median and lateral adductors of the mantle are absent.
5. The liver is divided.
6. The renal papillae are raised and chimney-shaped; they are situated near the anus in some Sepiidae.

Spirula thus shows relationships to all families of the Myopsida but there are also distinct differences.

The **Loliginidae** differ from *Spirula* in the following characters:

1. The gladius extends along the whole mantle, it is completely chitinized and a cone is absent.
2. The fins are triangular and are situated longitudinally along the posterior part of the sides of the mantle or extend along the whole sides of the mantle to the anterior margin.
3. The caecum is elongate and pointed.
4. The liver is undivided.
5. The beginning of the oviduct does not form a recurved loop.
6. Hectocotylization is restricted to the left ventral arm.

The **Sepiolidae** differ from *Spirula* in the following characters:

1. The shell is short, narrow, without calcareous deposits.
2. There is no tendency to a reduction of the closing apparatus, which results in a complete fusion between the funnel and neck cartilages in *Sepiadarium*.
3. The fins are situated in the middle of the sac-shaped body.
4. Median and lateral adductors of the mantle are present.
5. The liver is undivided and ends posteriorly in two processes.
6. Hectocotylization affects the dorsal arms.
7. The spermatophores are attached in a pocket of the mantle cavity.

The **Idiosepiidae** differ from *Spirula* in the following characters:

1. A shell is absent.
2. A closing apparatus of the neck is absent.
3. Median and lateral adductors of the mantle are present.
4. The tentacles are very small and barely as long as the ventral arms.
5. The posterior salivary glands are separate.
6. The liver has two processes.

465 The **Sepiidae** differ from *Spirula* in the following characters:

1. The fins are inserted laterally along the whole margin of the mantle.
2. The liver capsule is not completely closed.
3. The anterior salivary glands are only intrabulbar and the posterior glands are paired.
4. The oviduct does not form a recurved loop at its beginning.
5. The accessory nidamental glands are fused.

A study of the relationships between *Spirula* and the 4 families of the Myopsida shows that *Spirula* is distantly related to the Loliginidae, more closely to the Sepiolidae and particularly closely to the Idiosepiidae and Sepiidae. *Spirula* shows the following primitive, i.e. ancient characters: a chambered shell, traversed by a siphuncle; a free cartilaginous closing apparatus; the condition of the salivary glands typical for the Oegopsida; distinct separation of the ganglia of the central nervous system. Of particular importance is the large distance which separates the buccal ganglia from the posterior centers, as well as the length of the commissures. More recently acquired derivative characters, present only in the higher Myopsida, are the divided liver, which is pervaded by the esophagus and the aorta; the development of a large luminous organ at the posterior end of the body; the position of the raised, chimney-shaped renal papillae; the hectocotylization of both ventral arms.

If these characters are interpreted phylogenetically, *Spirula* represents a branch which separated early from the ancient Myopsida and shows a number of very primitive characters; on the other hand, it shows structural relationships present only in the most highly specialized Myopsida. *Spirula* has several important characters in common with the more primitive Sepiolidae and Idiosepiidae, especially the early-closing muscular capsule of the liver, the condition of the pallial nerve, the structure of the anterior and posterior salivary glands, and the condition of the beginning of the oviduct. These primitive characters which *Spirula* shares with the simpler Sepiolidae and Idiosepiidae are, however, far less important than the divided liver which places Spirula near the Sepiidae. A natural position for *Spirula* in the system, therefore, is not in the Idiosepiidae, in which Steenstrup placed them, but as a separate family, the **Spirulidae**, as proposed by the early authors. The Spirulidae should be placed between the Sepiolidae and Idiosepiidae on the one hand, and the Sepiidae on the other. On the basis of my data, the family Spirulidae is defined as follows:

Spirulidae

Myopsida with an internal chambered, calcareous, spirally coiled shell situated in the median plane the turns of which are not contiguous. The siphuncle is situated ventrally and completely surrounded by calcareous necks. The mantle has a free cartilaginous closure ap-
466 **paratus and ends posteriorly in a circular swelling which surrounds a large terminal luminous organ. The fins are small, rounded, separate and almost terminal, their base extending dorsoventrally at the boundary between swelling and mantle. The head bears olfactory tubercles and large eyes with an open lid fold as in the Oegopsida. The arm apparatus is of medium size; the arms bear several rows of suckers to 6 rows at the base, and are connected by broad margins. The tentacles are only partly retractile and much longer than the arms. The club bears numerous rows of suckers. The funnel depressors are situated broadly on the completely closed muscular capsule of the liver; median and lateral pallial adductors are absent.**

The buccal ganglia are situated far from the contiguous ganglia of the central nervous system and are connected by long commissures. The stomach is smaller than the kidney-shaped caecum; the anterior salivary glands are still partly extrabulbar, the posterior glands are fused. The liver is completely separated, and its posterior part is situated in the end chamber of the shell; the esophagus and cephalic aorta pass obliquely between the two lobes. The pancreas is large, cluster-shaped, and enclosed in a thin membrane together with the caecum. The renal sac is traversed in the middle by the mid-intestine and opens through two raised, chimney-shaped, fleshy papillae near the anus. The oviduct forms a recurved loop with equally large arms; the accessory nidamental glands are separate. Both ventral arms of the male are hectocotylized and without suckers, the left (?) arm is larger than the right. Spermatophores are deposited between the grooves of the inner buccal lip.

12. Biology of *Spirula*

The problem of the function of the terminal knob has often raised the question whether *Spirula* leads a sessile or pelagic life. It is surprising that paleontologists and zoologists still accept the view of Rumphius (cf. above, p. 342), that *Spirula* lives attached to coral reefs and is broken loose only during stormy weather. I remember a conversation with Alexander Agassiz in which he vehemently defended this view and also stated that *Spirula* lives on reefs not accessible to man, because there is no other
467 explanation for the masses of shells on the beach. In fact, a sessile life as described by Rumphius is impossible, as we stressed above.

Later observers, especially Owen, considered the terminal knob as a sucker which makes attachment possible. The structure of the terminal knob, as above-described (p. 338), disproves this. The terminal knob is a luminous organ in my opinion; whether one agrees with this interpretation or not, *Spirula* certainly has no organ which makes a sessile life possible, unless such a possibility be attributed to the suckers of the arms; but in that case, it would be difficult to explain why only *Spirula* of all Cephalopoda should have gone over to a sessile life.

Even if *Spirula* does not lead a sessile life, this does not preclude the possibility that it lives on the bottom. Some probability for this view could be found in the fact that the *Challenger* and *Blake*

specimens were caught in a dredge. Our expedition, however, has proved the pelagic habits of many animals that were previously considered as bottom forms, and were even shown in popular books to be dug-in in the mud (the bizarre fish *Melanocetus* and others, for example). The extensive use of vertical nets proved beyond doubt that some organisms are not bottom forms but pelagic forms living in deep water. Finds of such forms on the surface in some catches with a trawl may be due to the fact that it operates as a large-mesh vertical net and brings pelagic forms to the surface that probably live high above the bottom. The occurrence of *Spirula* in the trawl catches in two expeditions is thus no proof of life on the bottom.

The other specimens of *Spirula* with soft parts were found on the surface. This cannot be their normal environment because of their extreme rarity. An organism the shells of which are found in masses on tropical beaches could be expected to be one of the commonest pelagic forms if it were a surface form.

Spirula is thus apparently a pelagic deepwater form which is sometimes found on the surface, like many bathypelagic species. Deep-sea organisms which live on the bottom are found very rarely adrift on the surface. This is occasionally the case with fishes and Cephalopoda which normally live in deep water.

The retina of *Spirula* apparently provides the only reliable indication on its mode of life. As noted above (p. 350), the pigment in our specimen (Plate LXIX, Figure 3) shows a typical state of dark adaptation, which is present only in bathypelagic Cephalopoda.

468 Our specimen, too, was caught under conditions pointing to the mode of life of a pelagic deep-water animal, namely, dredging at a depth of 594 m near the continental slope without touching the bottom; and sure enough, its contents consisted entirely of a few pelagic deep-sea forms.

Catches of *Spirula* recorded since 1910 confirm this. They were all made with vertical nets in the Canaries Current. Joubin (1910) described a larva of *Spirula* caught on a cruise of the *Prince of Monaco* in a net sunk to a depth of 3,000 m. In the same year, 1910, a large collection of juvenile and adult *Spirula* was obtained in the Canaries area by the *Michael Sars* Expedition directed by Dr. Johann Hjort and was placed at my disposal. It consists of 3 older stages and an adult *Spirula* of 26 mm mantle length. This valuable material was caught exclusively with vertical nets at depths between 300 and 4,000 m.

In view of all these records one can hardly consider *Spirula* as a sessile animal living on coral reefs or on the bottom of the deep sea. It is also difficult to assume that it occurs normally on the surface. Therefore, *Spirula* should be recognized as a pelagic deep-sea Cephalopod.

The air enclosed in the chambers of the shell apparently enables the animal to float in the water, just as is the case of the air-containing calcareous shell of the surface-inhabiting cuttlefishes. When a *Spirula* dies, its soft parts decay and the shell rises to the surface because the enclosed air cannot escape, except perhaps from the initial chamber. Shells of *Spirula* have not been found in deep-sea sediments. They always come to the surface, where winds and currents carry them until they are finally driven ashore and accumulate there. The mass occurrence of shells of *Spirula* in some areas suggests that it is common in deep water but, being a good swimmer, usually avoids the nets.

13. Postembryonic development of *Spirula*

In the preceding chapters we mentioned larvae of *Spirula* known since 1910. Joubin (1910) published an interesting report on a larva caught in 1904 on a cruise of the *Prince of Monaco* in a

vertical net sunk to a depth of 3,000 m. The locality was near the Canaries (south of Ferro), i.e., that part of the Canaries Current where later, in 1910, the *Michael Sars* Expedition under the direction of Johann Hjort caught the most magnificent material of *Spirula* ever obtained. It consists of 8
469 specimens, comprising larvae and other juveniles or almost adult specimens. They were caught with open nets at depths between 300 and 4,000 m; I described and illustrated them in the report on the scientific results of the *Michael Sars* Expedition (1913) and it is here presented by courtesy of Dr. Hjort.

Though the material had, naturally, to be treated with care, I later made sections of the youngest larva (Plate LXXIII, Figure 1). The description will thus be divided into two parts, the first dealing with the form of the larvae and juveniles, the second, with their anatomy. Moreover, I note that the material was also examined by an outstanding authority on the Cephalopoda, Dr. Naef of Naples, during a visit to Leipzig. Dr. Naef published his results in a brief but very instructive communication *Studien zur generellen Morphologie der Mollusken*, Part 2: *Das Cölomsystem in seinen topographischen Beziehungen*, "Zur Anatomie und Entwicklung von *Spirula australis* Lam." (1913) (Studies on the General Morphology of Molluscs, Part Two: The Coelomic System and its Topographical Relationships, "On the Anatomy and Development of *Spirula australis* Lam.").

The juvenile stages were fixed in formol and then transferred to alcohol. This procedure was successful for the young stages; the older stages, however, had been damaged during capture, and not by the preservation, as already mentioned in the chapters on the coloration.

The youngest larva (Plate LXXI, Figures 1, 2) was caught in a net sunk to a depth of 1,000 m. It has a plump, barrel-shaped body with 5 externally visible chambers at the posterior end. The chambers are—as also noted by Joubin about his specimen—completely covered by the mantle, which is very thin in this area. The shell had 6 chambers (Plate LXXIII, Figure 1). There is no thickening or distinct pigmentation at the posterior end. Sections show, however, the first indications of proliferation of cells which later form the terminal disc. The margin of the mantle is straight and has no dorsal or ventral corners. Of special interest is the position and small size of the fins. They are spatulate, 0.6 mm wide and long, and separated by the width of the terminal chambers. The bases of the fins are situated steeply in an anteroposterior direction and do not reach the posterior end of the body beyond which the fins do not project.

The head of the larva projects from the mantle margin, so that the wide funnel extends to the
470 base of the arms. The eyes are small, oval and only 0.26 mm long in longitudinal diameter. The small size of the eyes was already noted by Joubin.

The arms are completely developed, but the 4th arms form only small stumps. The 1st and 2nd arms are of about the same length, the 3rd arms are slightly smaller. There is no trace of tentacles. Since the tentacles of the adult can be retracted into a sheath, I assume that "anlagen" are already present. The pointed jaws protrude slightly, and push the inner lips and buccal membrane aside.

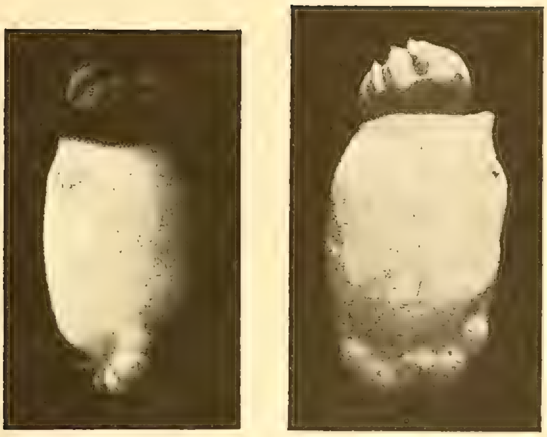
The larva is more intensively pigmented only on the head. Here are dense, light-brown chromatophores with a slight purple tinge. Funnel and arms are without chromatophores. Only a few chromatophores are present on the mantle. The mantle margin does not show dense chromatophores but chromatophores are slightly more numerous at the posterior end near the shell and the whitish fins.

The older stages (Figures 3, 4, 5, 6) are described briefly as they show mainly the same relationships.

The mantle is still barrel-shaped, without corners at the free margin. The shell becomes more distinct at the posterior end of the body and consists of 6 or 7 chambers which are most distinct in the largest larva (Figures 5, 6). The siphuncle is visible through the chambers at some points. The

FIGURE 42. *Spirula*, youngest larva

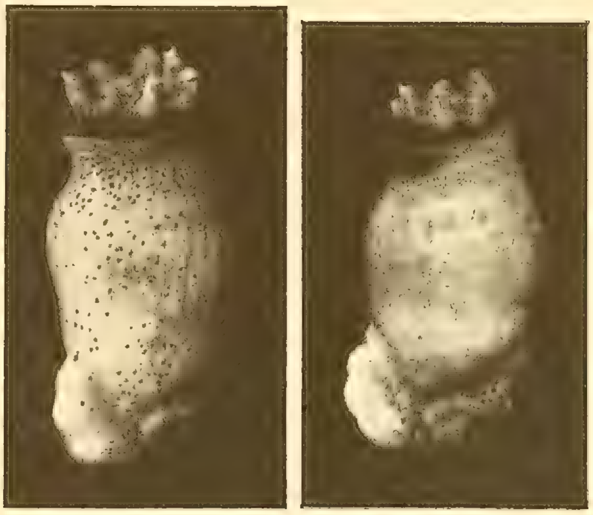
Length 6 mm. The shell consists of 6 chambers, of which 5 are visible. Ventral view.



a b

FIGURE 43. *Spirula*, medium-sized larva

a ventral view; b lateral view. Six chambers of the shell are visible.



a b

FIGURE 44. *Spirula*, older larva, of 8 mm dorsal mantle length

a ventral view; b lateral view.

shell is covered with the thin outer skin, which in these stages is more strongly pigmented in the posterior region than it is in the youngest stage. The pigmentation increases at the mantle margin and extends gradually to the base of the arms. The fins are only slightly larger but their position is the same. As the
471 head is retracted deeply into the mantle, the tentacles of all the older larvae are not visible, although the arms of the oldest larva were spread and the tentacles could not have escaped one's notice.

A condition already indicated in the youngest larva becomes more distinct. The mantle thickens slightly at the chambers of the shell and near the base of the fins, indicating the boundary of the ovals; the latter become more distinct later, on the dorsal and the ventral side.

The juvenile form illustrated in Figure 7 shows marked progress, compared to the 3 larvae described above. It has a dorsal mantle length of 12 mm, compared to 8 mm in the older larva (Figures 5, 6). The dorsal and ventral corners of the mantle are present for the first time, although they are rounded and project little. The fins are slightly larger; they are 2 mm wide at the base, and extend obliquely anterodorsally to postero-ventrally. Though the fins are 3 mm wide, they do not

project beyond the posterior end. The mantle margin and posterior end are more strongly pigmented than they are in the earlier stages. As noted above (p. 328), the middle of the mantle is only weakly pigmented, but this area was partly preserved in only one of the older stages; it was chafed off in the other specimens, so that the silvery layer of the cutis was exposed.

The form of the posterior end of the body is of special interest. It is light-colored and contrasts with the strongly pigmented surrounding part; the first indication of the whitish conical structure which I interpreted as a luminous organ is visible in its center (Figure 8). A slight thickening surrounds it. The specimen is slightly damaged but the chambers are not exposed and are covered with a thin membrane. The mantle margins around the shell have become thicker and the ovals under the thin membrane are therefore more distinct.

The eyes have become much enlarged; they project laterally beyond the mantle margin and are almost completely covered by the lid fold, which is nearly closed. The eye is at least 2 mm wide. The arms are slightly better developed than in the earlier stages but still without the intensive pigmentation of the other parts of the head.

The other young specimens of *Spirula* gradually become more similar to the adult (cf. Text Figures 35, 36, 37, pp. 328, 330). The tentacles project only slightly between the arms. The eyes become larger and the mantle corners become more marked, the ventral corners beginning to surround the
472 funnel. The posterior end begins to resemble its definitive condition. The whitish cone of the luminous organ becomes more distinct and around it develops a thick, colorless swelling that borders on a central depression which surrounds the luminous organ. This is illustrated in Text Figure 46 of the posterior end of a specimen of 18 mm dorsal mantle length from Station 42. The pigmentation here is more intense at the circumference of the lightly pigmented tip and extends dorsally and ventrally over the chambers and the base of the fins, which until now were not pigmented. The main characteristics of

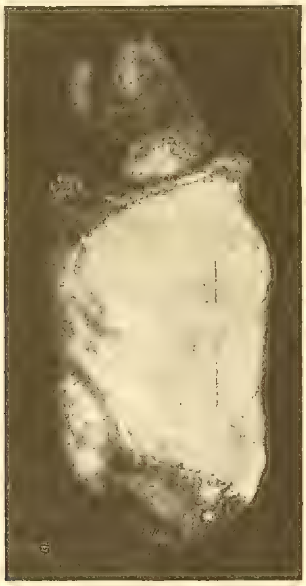


FIGURE 45. *Spirula*, juvenile stage of 12 mm dorsal mantle length

Lateral view (dorsal side on the left).

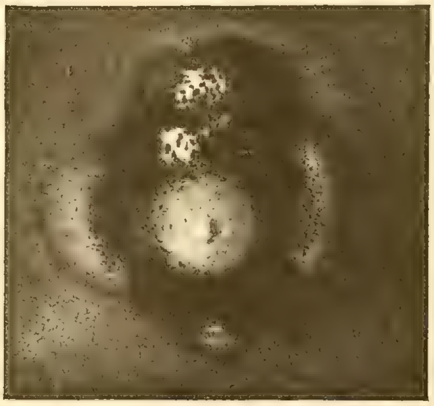


FIGURE 46. *Spirula*, juvenile stage (cf. Text Figure 35, p. 328)

Posterior end. The dorsal surface is rounded upward.

the young *Spirula* are thus the development of a depression around the luminous organ, the development of folds on the arms, and the more projecting tentacles.

I would like to comment again on one aspect which I already described for the adult *Spirula* caught by the *Valdivia*: the shell is never freely exposed on the dorsal or ventral side. In all specimens of *Spirula* the very thin mantle covers the shell in the area of the ovals. Some of the chambers were exposed only in the oldest specimen, because of damage. The torn margins of the membrane were clearly visible around the exposed chambers; this is the result of an injury of this delicate area. JOUBIN considers the exposed chambers as a normal condition in his description of the youngest larva, but he explains this condition more convincingly than PELSENEER. Having now proved also for the adult that the chambers of *Spirula* are never freely exposed, the view that *Spirula* has an outer shell should be finally discarded.

14. Sections of the youngest larva*

Though I hesitated to section this valuable material, I did so nevertheless, because of the valuable
473 information which sections provide. Longitudinal sections of the youngest larva (Plate LXXI) were made by my student STICH. The sections were given to Dr. NAEF, who reported on them briefly in his study of the coelom of the Cephalopoda (1913). Figure 1 of Plate LXXIII is a median section with details added from adjacent sections. Since the walls of the shell had slightly shrunk in the section, the arrangement of the chambers was drawn after the cleared specimen before sectioning. The outer form has been described in the description of the larva (p. 362).

The **mantle** consists of 3 layers: an outer layer (Plate LXXIII, Figure 1, *pall. e*) of medium thickness, a thin inner layer (*pall. i*) facing the respiratory cavity, and a thick intermediate layer (*pall. m*). The outer and inner layers are fused at the margin but differ in structure. The outer layer consists of longitudinal fibers and passes toward the posterior end of the body into a cutis with scattered juvenile chromatophores. The thin inner layer contains isolated circular fibers covered with delicate longitudinal fibers toward the mantle cavity.

The intermediate layer (*pall. m*) shows larval characters; it does not yet contain a compact system of fibers and consists mainly of a gelatinous substance in which central bundles of circular fibers are seated that are distinct already in the cleared larva. The bundles become gradually thinner toward the attachment of the shell and the free margin of the mantle. They are crossed by isolated longitudinal fibers with branched ends.

* Professor CHUN had prepared and submitted his manuscript for publication as far as the description of the anatomy of the youngest *Spirula* larva, when death interrupted his work. A large part of the manuscript was fortunately found among his papers, complete and partly revised; only references to the figures had to be inserted. The plates were completed and revised up to Plate 93 and the figures for Plate 93 were also indicated. The following parts were incomplete or absent: the anatomy of the youngest *Spirula* larva, the description of the Bolitaenidae, *Amphitretus*, *Vampyroteuthis*, *Opisthoteuthis*, and some species of *Polypus*. Preliminary communications and notes of Professor CHUN were used to complete some of the descriptions, while others had to be written anew. This was done by Professor THIELE of Berlin and Dr. WÜLKER of Heidelberg. Their help has made it possible to complete the last work of Professor CHUN and to both of them I express my sincere gratitude.

Professor CHUN probably intended to extend some chapters, to revise and expand the results given in the preliminary communications, to consider data published since, and to summarize his results and use them for the discussion of general problems. I preferred, however, to let him speak for himself in his last major work, without adding further complementary material.

A. BRAUER

Shell

The structure of the mantle is strongly influenced by the chambered shell. The mantle flattens markedly toward the shell and passes abruptly into the outer lamella of the shell sac. Sections show
474 that the outer lamella of the shell sac is very thin and without muscular fibers. The epithelial lamellae are very thin and enclose a thick cutis which again contains isolated chromatophores.

The outer lamella of the shell sac forms a slight thickening (Figure 1, *a*) at the level of the third to last chamber, near the anterior margin of the septal border. This thickening is caused by an epithelial layer with rounded nuclei which adheres closely to the wall and gradually flattens laterally. A thin slit separates the thickening from the shell sac. The significance of this epithelial thickening is not known. It may develop later into the large, pad-like thickening at the posterior end that forms the terminal disc (p. 337ff.). It may also be the last rudiment of the rostrum, which is well-developed in the fossil *Spirulirostra*.

The shell consists of 6 chambers, a rounded initial chamber with a distinct prosiphuncle (Figure 1, *pros*), and 5 chambers which become successively larger. The shell of the larva is identical with that of the adult in all details. The walls are secreted by the epithelium of the outer shell sac, but the septa are secreted by the inner lamella of the shell sac. The margin of the living chamber, where the two lamellae of the shell sac pass into each other, shows already a cartilage on the dorsal side on which the musculature of the liver capsule is inserted. This cartilage extends far anteriorly on the dorsal side, to about the level of the renal papilla. It descends ventrally and reaches to near the opening of the esophagus (*oes*) into the stomach (*st*). The inner wall of the shell sac adheres closely to the living chamber and shows at the entrance to the siphuncle the characteristic thickening of the epithelium with high cylindrical cells which was described for the adult *Spirula* (pp. 336, 337). Behind the entrance to the siphuncle the cells again become flatter and finally form the peculiar, almost spongy tissue which secretes the siphonal necks. The siphuncle is living tissue which extends through the entire length of the siphonal necks, not being reduced even in the initial chamber. At the entrance to the siphuncle the cylindrical epithelium is covered with a pad of cells which are apparently mesodermal and separate the siphuncle from the liver. A thin epithelial lamella covers this structure toward the liver. Naef (1913) stated that the siphuncle contains a central canal with a relatively small, funnel-shaped opening in the center of the living chamber. He considered this canal as part of the body cavity because the funnel-shaped opening opens into a part of the body cavity between the posterior margin of the liver and the inner lamella of the shell sac. He thought that this coelomic space communicates with the general body cavity which surrounds the intestinal tract. I am not sure that this is
475 correct. The space labeled "*x*" in Figure 1 is probably caused by the preparation for sectioning. Nor am I sure that this coelomic space communicates with the body cavity, because the assumed place of communication shown by Naef in the drawing is plugged by a gelatinous tissue which contains blood vessels and borders on the visceral sac. However, the canal inside the siphuncle probably represents part of the body cavity. This assumption is supported by the distinct funnel-shaped opening and by the histological structure of the tissue which lines the canal.

As far* as can be determined by the condition of the specimen and the weak differentiation of the delicate juvenile tissue, the epithelial layer (coelothelium) which lines the coelom continues without change of its structure into the epithelium of the siphonal coelom. In the siphuncle of the adult, on the other hand, none of the cross sections of the vessels (Plate LXXIII, Figure 2) is with certainty

* The following text on *Spirula* was written by Dr. G. Wülker (Heidelberg).

interpretable as a cross section of the siphonal coelom. This does not disprove the observation made in the larva, because it is possible that the coelomic canal of the siphuncle, which was considered by Naef as a primary character of early phylogenetic stages of the Cephalopoda, becomes reduced during individual development.

In addition to the characters of the mantle and the shell, the median sections through the larva, too, give information on the development of the **cephalopodium** (head with arms and funnel) and of the **inner organs.** On the whole, the definitive conditions are already distinctly developed.

The head projects from the anterior margin of the mantle. It encloses the buccal mass and bears 8 well-developed **"anlagen" of the arms,** of which the first two pairs (p^1) are slightly larger (p. 326) and already bear small suckers. The longitudinal sections do not show the retracted tentacles. Lateral sections (not illustrated) show the small **"anlagen" of the eyes**, which already have an iris, a retina and a lens, and also the open lid fold which resembles that of the Oegopsida and is characteristic for *Spirula*. The **funnel** (*inf*) projects slightly from the mantle, ventral to the buccal mass. The funnel valve (*valv*) is situated opposite the small opening of the funnel. The section also shows parts of the funnel organ of which the figure shows the unpaired dorsal part (*o. inf. d*) and one of the paired ventral parts (*o. inf. v*). Dorsally between the mantle and the muscular capsule of the liver is situated another part of the funnel apparatus, i.e. the collaris (*coll*), which is connected in the section by a narrow band with the liver capsule, while the free margin of the muscle projects into the dorsal part of the mantle cavity. The section also shows several large chromatophores near the funnel.

The cross section of the **intestinal tract** shows the buccal mass, with delicate "anlagen" of the buccal membrane, lips and jaws (*mx. sub*, *mx. inf*). The pocket of the radula and traces of the weakly
476 developed anterior salivary glands (buccal glands) are visible on the dorsal side of the pharynx. Ventrally there is also an unpaired "anlage" of the gland, which corresponds to the submaxillary gland of the Cephalopoda. Slightly dorsally opens the efferent canal of the posterior salivary gland which is visible as a structure fused to singularity, in front of the liver. Also visible is the esophagus, which passes between the halves of the liver, and its opening into the stomach; the caecum is visible only in lateral sections. The short rectum with the "anlage" of the ink gland is situated in the middle.

Of the nervous system, one can see only the large centers that are already concentrated in a central ganglionic mass around the esophagus, the two esophageal ganglia, the "anlage" of the static organ (*stat*), the gastric ganglion (*g. gast*), and one brachial nerve at the periphery.

The section also shows the heart, kidney and gonad. The gonad is still in an early stage of development, but the specimen is apparently a female. Examination of the **genitalia** shows another important condition which was also stressed by Naef: lateral sections show "anlagen" of the oviduct glands on both sides, although the mature animal has only a single oviduct on the left side. This and the analogous data of Döring (1908) for *Sepia* and *Loligo* suggest that the oviducts were originally paired in the ancestors of the Myopsida and became restricted to one side of the body only in the course of phylogeny. The conditions of the coelom have been discussed above (p. 366).

Of particular interest is the well-developed **muscle** (*mu. umb*) which extends from the posterior lower side of the liver capsule to the umbilious of the shell and is a unique character of *Spirula* in the Myopsida.

The sectioned larva of *Spirula* thus shows—beside many traits of a nearly definitive condition—some larval characters which suggest that it belongs to the recent Myopsida; it has, however, some special characters, unique to it (coelom, shell), which suggest that it should be given a separate position in the group and which give rise to the assumption of a closer relationship to a postulated common ancestor.

Octopoda LEACH, 1818

Argonautidae CANTRAINE, 1841

Argonauta LINNÉ, 1758

Argonauta hians SOLANDER
(Plate LXXIV, Figures 1, 2, 4–6)

We collected two juvenile *Argonauta*, a male (Figure 1, 4, 5) and a female (Figure 2, 6) in a vertical net in deep water in the area of the South Equatorial Current (Station 50). These specimens closely
477 resemble *Argonauta hians* in characteristic form. The shell of the female was lost, but the proportions of the body and some characters of the apical suckers of the arms closely resemble an adult, well-preserved specimen of *A. hians* examined. The young male, the 3rd left ventral arm of which was hectocotylized and coiled in its cutaneous pocket, is of special interest, since the male of this species was not known until now.

The female, which is larger, has a dorsal mantle length of 6.5 mm and a head width of 5.3 mm; the corresponding measurements of the male are 5 and 4.2 mm. The mantle is sac-shaped, with a broad slit which extends beyond the middle of the eye in the female. The funnel is narrow and almost reaches to the base of the arms. Funnel and mantle cartilages of male and female are shown in Figures 4 and 6.

The **eyes** are relatively large; the small olfactory tubercle projects distinctly at the posterior margin of the eye. The **arms** are connected at the base by thin outer margins; the dorsal pairs of arms of the female are longer than the others and have a broad margin which secretes the shell; this margin became strongly contracted during preservation. The suckers of the arms are biserial; the apical suckers of the arms of the female are flattened, but not as markedly as in another female examined which had a mantle length of 15 mm. This specimen had 8 raised proximal suckers on the 1st and 2nd arms and 7 such suckers on the 3rd and 4th arms, which are followed by the flattened suckers at the tip.

The coloration is not very vivid and is caused by two layers of chromatophores. The superficial chromatophores of the male are uniformly distributed on mantle and head, those on the dorsal side are slightly more strongly contracted. They are more numerous on the membrane enclosing the hectocotylus. The deeper layer of chromatophores shines through at the posterior end of the body and on the head, which bears about 6 symmetrically arranged pairs of chromatophores on each side. The chromatophores on the outer side of the arms are scattered and form two indistinct lateral rows; almost every stalk of a sucker shows a chromatophore. The female shows a similar pigmentation, but the superficial and deep chromatophores near the eye form nearly concentric circles, and the arms and stalks of the suckers bear some smaller chromatophores, in addition to those present in the male. The lobes of the arms bear numerous dotlike chromatophores which gradually disappear toward the tip.

Argonauta sp.
(Plate LXXIV, Figure 3)

A surface catch near the Somali coast (Station 263) collected a juvenile female of *Argonauta* which differs from the young *A. hians* described above in its plump, short, sac-shaped mantle and especially in its vivid coloration. The arms of this specimen were folded back; they had outer membranes at
478 the base of all arms and broad membranes on the dorsal arms. The dorsal mantle length was 6 mm, the ventral mantle length 4.2 mm. The total length to the jaws was 7.8 mm and the greatest width of the mantle 4.5 mm. The eyes are relatively large; the small olfactory tubercles are visible distinctly on the base of the mantle. The funnel projects beyond the anterior margin of the eye. Its cartilage resembles that of the young male of *A. hians* (Figure 4); it flattens posteriorly and a trace of a tragus seems to be present. The opposite cartilage of the mantle is conical, as in *A. hians*.

The vivid coloration is caused by two layers of chromatophores, most of which are expanded. The chromatophores are slightly darker and less dense dorsally and around the eyes than on the ventral side. The chromatophores form two rows on the outer sides of the arms, and there are a few scattered chromatophores between them. The bases of the suckers bear several chromatophores and there are numerous chromatophores also on the inner side of the arms, between the suckers and on the inner side of the membrane which connects the arms.

Philonexidae d'Orbigny, 1838

Tremoctopus delle Chiage, 1830

Tremoctopus hyalinus Rang
(Plate LXXVII, Figures 1, 4–6)

We caught a juvenile *Tremoctopus*, which I identify as *T. hyalinus*, in a vertical net in deep water in the South Equatorial Current (Station 49). Its dorsal mantle length is 4.5 mm and the head width is 5 mm, like the mantle. It belongs to *Tremoctopus* because the arms are of different length. The arm formula is 1, 2, 4, 3. The sac-shaped **mantle** has a broad slit which extends beyond the middle of the eyes. The eyes are relatively large and resemble those of the Oegopsida as they have only a simple lid fold at the periphery of the lens. The eyes protrude so markedly that nearly the whole eyeball is situated on the surface. The olfactory tubercles are distinct behind the eyes near the base of the mantle. There is a small knob near the olfactory tubercle on each side at the base of the mantle.

The ventral side of the mantle was strongly contracted, so that the funnel and the anal region were exposed. The background of the funnel (Figure 5) is concave and shows a groove which indicates the border between collaris and funnel. The anus has spatulate appendages and is surrounded laterally by the long arm of the median mantle adductor. The closing apparatus is formed by folding up of
479 the lateral margins of the funnel, toward which the funnel depressors extend. Into these two pockets, which are open anteriorly, projects a swelling of the mantle which forms a shallow curve behind the ventral margin of the mantle. There is thus no conical mantle cartilage like that in *Argonauta*.

The pigmentation of the mantle is weak. The ventral side of the mantle has almost no pigment, except for a row of chromatophores near the margin. There are 4 symmetrically arranged pairs of chromatophores and a median chromatophore on the dorsal side of the head. More numerous chromatophores are present around the eyes. Only the margin of the funnel bears chromatophores, two on each side. The outer side of the arms bears 4 chromatophores in a row at the base, but there are only 3 such chromatophores on the 2nd arms. These are followed by two rows of chromatophores, on the 1st and 2nd arms, while the 3rd and 4th arms show the bifurcation of the basal row of chromatophores. There is also a chromatophore on the inner and outer side of the base of each sucker.

I consider this young specimen as belonging to *Tremoctopus hyalinus*, mainly because of the large, protruding eyes. Other juvenile specimens of *Tremoctopus*, e.g., *T. microstoma* Reynaud (Joubin, 1893), have sessile eyes, and the protruding eyes are a specific character of *T. hyalinus*, which was described by Férussac and d'Orbigny. I examined a specimen 15 mm long from the collection of Carus. The specimen is a male of 6 mm dorsal mantle length; its eyes completely protruded through the lid fold; the 3rd right arm was hectocotylized and coiled inside a skin fold. The closing apparatus of the funnel is almost identical with that of the young female described above. The head is 6.2 mm wide, wider than the mantle. The dorsal arms are 8 mm long, the 4th arms 3.2 mm.

Octopodidae D'ORBIGNY, 1838

Velodona n. gen.

Velodona togata n. sp.

(Plates LXXV and LXXVI and Text Figures 47 and 48)

Trawling at a depth of 749 m at Station 249 near the east African coast, we collected a large octopod of peculiar habitus. The specimen has a sac-shaped body and very large eyes. Its arms are folded back and have very large membranes which enclose the whole animal. It was alive and we made color sketches. Its characteristic form is illustrated on Plates LXXV and LXXVI, which show the characteristic
480 pale coloration of the animal and also the very wide membranes. The specimen was preserved in formol and later transferred to alcohol. The strong contraction of the membranes is shown in the photographs (Text Figures 47 and 48).

The specimen is a male which resembles the genus *Eledone* in the presence of a single row of suckers on the arms. However, it differs from *Eledone* not only in the unusually large membranes, which show some special characters, but also in the structure of the hectocotylized 3rd right arm. The hectocotylus of *Eledone* is extended, that of this specimen is curved into a narrow *S*. The funnel organ has a characteristic form and differs distinctly from that of *Eledone*.

I named the genus *Velodona* and the species *V. togata* because of the very large membranes of the arms.

The **mantle** is plump, sac-shaped, rounded posteriorly and wider than long. It is 99 mm wide and has a ventral length of 80 mm in the preserved specimen. The broad, transverse slit of the mantle extends to the posterior ventral margin of the large eyes. The whole funnel is exposed because of the
481 contraction of the mantle margin. It is conical and its opening is situated more or less at the level of the anterior margin of the mantle; it is folded broadly anteriorly on each side, forming two deep grooves between the stiff, folded-over margins. These margins fit into corresponding depressions of the mantle and thus form an effective closing apparatus.

The **eyes** are unusually large—a fact that indicates life in deep water—and enlarge the head so that it is as wide as the mantle. The eyes are 38 mm wide and 53 mm long. The pupil was sickle-shaped in life and the interior of the eye was blackish. The lid fold is sharply defined at the ventral margin; it flattens laterally and continues dorsally in a thin transparent seam which extends almost to the ventral lid fold in the preserved animal.

Small warts cover the whole dorsal surface of the mantle and head and the outer side of the proximal half of both dorsal pairs of arms. The tentacles are situated dorsally at the level of the middle of the eyes. The tentacles were raised like feelers in the live animal, but they are strongly contracted in the preserved specimen. Two larger warts are situated at the base of the dorsal arms. The warts
482 are arranged in crossing curves on the mantle and eyes, but there is no regular pattern. There are both moderately large and very small warts between the large warts. All warts are covered with whitish conical tentacles, 10–13 on the large warts and a single tentacle on the small warts, with transitions between the extremes.

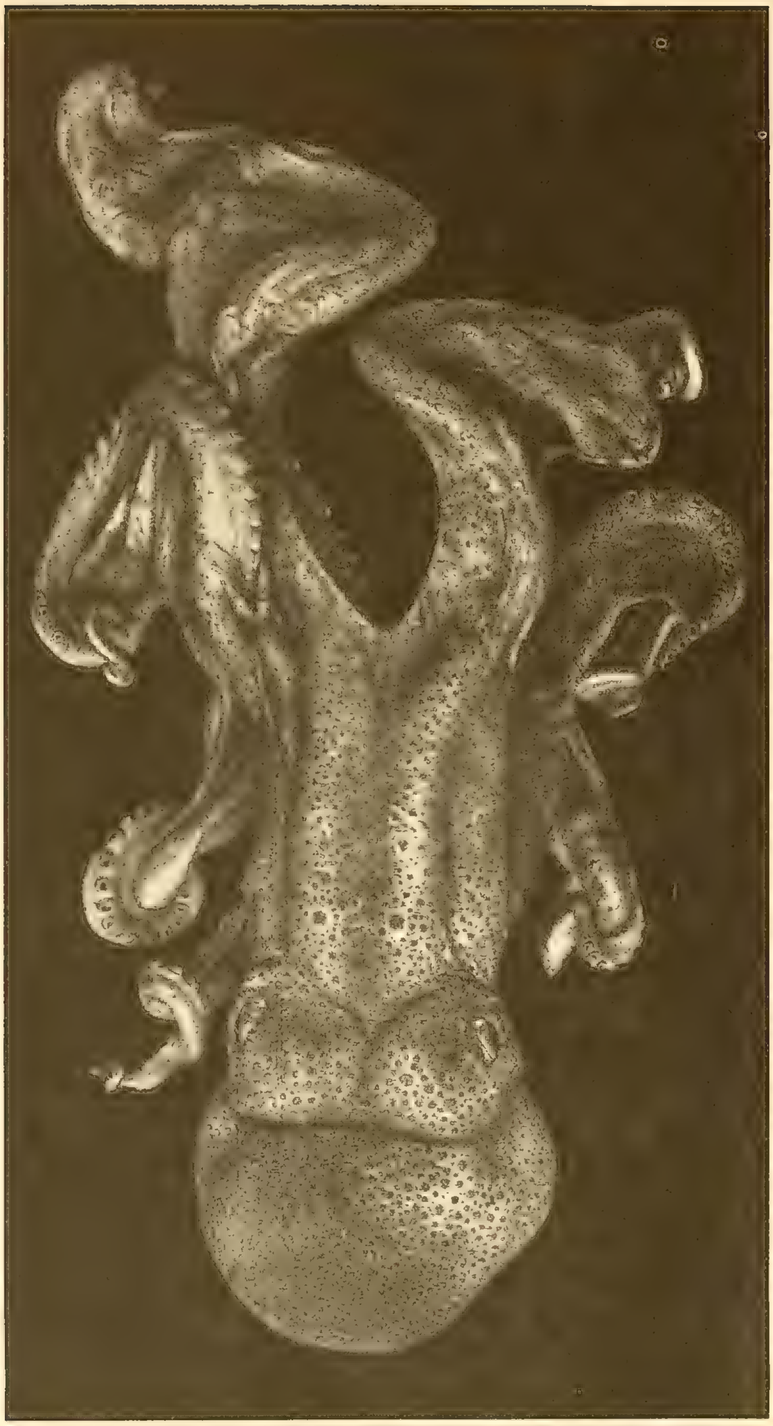


FIGURE 47. *Velodona togata*

The **arms** are well developed. They decrease in length from the dorsal to the ventral arms. Because of the contraction of the muscular membranes, the arms of the preserved specimen were coiled at the tip, so that it was difficult to measure them. I therefore measured their relative length by counting the uniserial suckers, which was also difficult because the membranes extended on the arm and prevented their spreading. The number of suckers on the left arms was as follows:

FIGURE 48. *Velodona togata*

Dorsal arm	102 suckers
2nd arm	88 suckers
3rd arm	82 suckers
4th arm	77 suckers.

Along the hectocotylus there were only 45 suckers up to the spoon-shaped tip, not including the very small suckers on the tips of the arms.

The arms bear dorsal and ventral membranes. The ventral margins are unusually large and extend to the tip of all arms. They are not restricted to the ventral surface but also extend to the dorsal margin

of the neighboring ventral arms, where they again continue to the tip, but are more weakly developed.

The two dorsal arms are connected proximally by dorsal membranes which extend to the proximal third of the arm. The ventral membranes of the 1st arms are the largest and their free margin shows a swelling caused by longitudinal muscles. They envelop the body like a toga. They continue much narrower on the dorsal side of the 2nd arms and extend there to the tip, so that they form a groove with the ventral membranes of the 2nd arms.

The same applies to the ventral membranes of the 2nd and 3rd arms. They become successively narrower but also pass to the dorsal outer margin of the following arms and form a groove with their ventral membranes.

The ventral membranes of the 4th arms are connected broadly with each other at the base of the arms and thus form the counterpart of the dorsal membranes of the 1st arms.

The transformation of the right 3rd arm into a **hectocotylus** (Text Figures 49 and 50) is caused
483 by modification of the condition described above. The hectocotylus is much shorter than the other arms and bears only 45 suckers up to the spoon-shaped tip. The shortening is caused mainly by the *S*-shaped curvature of the distal part of the arm, a condition that has not been observed in the related genus *Eledone.*

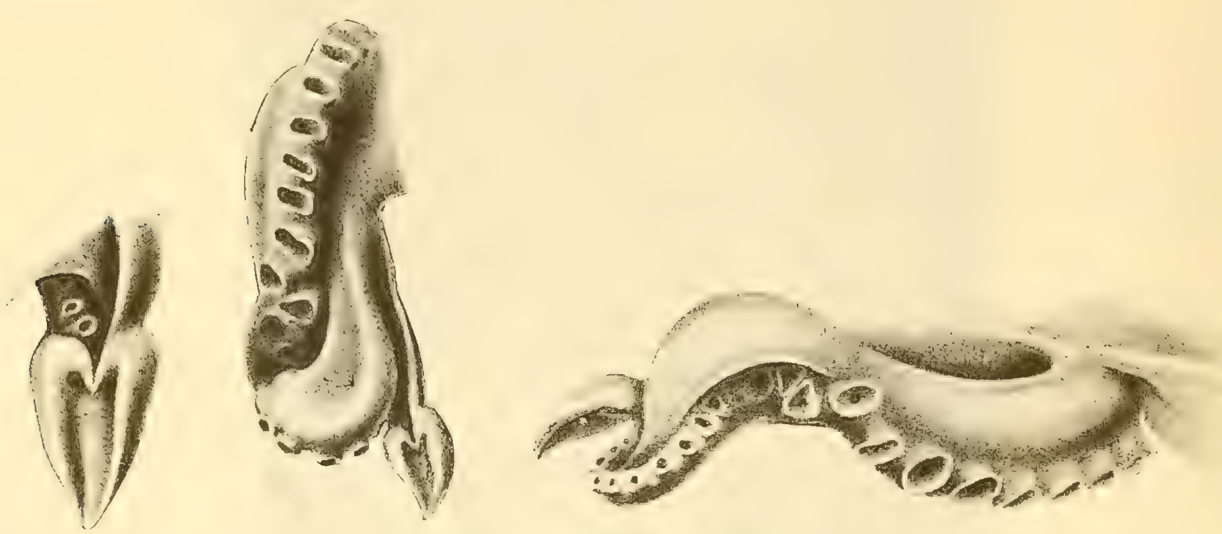


FIGURE 49. Hectocotylus of *Velodona*

The ventral membrane of the 2nd right arm passes to the outer side of the hectocotylus but does not reach to the tip. The ventral membrane of the hectocotylus is well developed and forms a deep groove for the spermatophores from the spoon onward, which gradually flattens into the normal ventral membrane which continues on the dorsal outer side of the 4th arm, where it soon disappears.

The spoon-shaped terminal part ends in a sharp point. It is convex on the outside and has a pit on the inner side which is bordered by swollen margins that become narrower toward the tip. The spermatophore groove projects in scabbard-like form at the base of the spoon and is bordered by the inward-curved margins of the spoon. The transverse folds on the inner surface of the spoon are weakly developed; there are about 15 transverse folds some of which are interrupted in the middle.

FIGURE 50. Hectocotylus of *Velodona*, photographed in natural position

Mantle complex

Opening of the mantle cavity from the ventral side (Text Figure 51) shows that the mantle margin thickens toward the suspensorium of the gills and forms a sharply defined swelling. The depression
484 thus formed behind the mantle process contains the folded-over posterior margins of the funnel and thus forms a mechanism for closure. The thick median mantle adductor surrounds the slightly projecting rectum, and its folds are visible through the anus. The muscle then extends broadly into the mantle, where it is 35 mm wide at the base. The anterior lateral adductor of the mantle is visible at the level of the tip of the gills and its insertion in the mantle is situated dorsal to the anterior end of the branchial gland.

The funnel depressors are relatively short and thick; they widen toward the fold of the closing mechanism of the funnel and continue laterally to the mantle.

The gills are thick, 30 mm long, with 8 broad lamellae on each side. Near the base of the gills are situated the chimney-shaped renal papillae which are 4 mm long. The branchial hearts, which are 16 mm wide, are pushed to the side. To the left of the median mantle adductors is situated the end of the spermatophore sac which does not project freely into the mantle cavity, but its dorsal surface is broadly connected with the mantle. From the opening of the spermatophore sac projects a whitish spermatophore; I was able to extract a 55 mm long part of it from the gonoduct. Its posterior end was broken off and its outer membrane was already rather coarse and elastic. The male gonoducts were indistinctly visible through the thick abdominal wall. The olfactory pit was visible as a slit at the point where the anterior margin of the mantle is attached to the body and the collaris extends into the mantle.

FIGURE 51. *Velodona togata.* Opened mantle cavity.

The **funnel organ** of *Velodona* is not divided into 3 parts but consists of two symmetrical parts which are not very large. The two parts are situated 3 mm apart; each consists of two broad lobes which are broadly fused posteriorly.

This funnel organ corresponds to that of type *D* of Jatta's classification (1896, p. 23) and present
485 also in *Scaeurgus tetracirrus*: it consists of two parts which form an angle; in the latter these two parts are, however, not as widely separated as in *Velodona* and are also much narrower. Comparison with other funnel organs shows that the single dorsal part has become divided into two halves which are fused broadly with the symmetrical lateroventral organs. Each part is 13 mm wide; the parts near the median line are 12.5 mm long.

This funnel organ differs markedly from that of *Eledone*, in which the dorsal part is entire and not divided into halves.

Polypus Lamarck, 1799

Polypus valdiviae (Chun, MS) n. sp.
(Plate LXXX and Text Figures 52, 53)

by Professor Dr. J. Thiele (Berlin)

Locality: Station 103: 35°10.5′ S, 23°2′ E. Trawl, 500 m. Agulhas Bank.

Three of the 4 specimens caught are females and one is a male. The species has been named by Chun. However, Eydoux and Souleyet (*Voyage de la "Bonite"*, Vol. 2, p. 11, *Moll.*, Plate 1, Figures 6, 7) illustrated a small specimen from the Cape of Good Hope naming it "*Octopus capensis*"; it was probably a juvenile and was incompletely characterized—perhaps it is identical with our species.

At any rate, *P. valdiviae* is related to two species from the west coast of the Sahara: *P. ergasticus* and *P. sponsalis* P. *et* H. FISCHER (cf. H. FISCHER and JOUBIN, *Expéd. Travailleur "Talisman"*, Vol. 8, p. 322ff.) which have a similar hectocotylus.

The coloration is reddish brown dorsally and light-brownish ventrally; it is caused by numerous dotlike chromatophores which are dense dorsally and sparser laterally and ventrally, where they are hardly visible without magnification. The dorsal side of the body and arms is covered with flat, indistinct warts which are much larger above the eyes, and one wart above the eye is so much larger that it forms a small cirrus.

The sac-shaped body is markedly broader than high, slightly flattened dorsally. The head is as wide as the body and the eyes are large. The mantle margin is slightly concave and about 2 cm long. The suckers are small, most of them markedly raised. They alternate on each arm in 2 rows and the suckers at the tip are very small and indistinct. The mouth is surrounded by a folded membrane, but there is no ring-shaped lip. The funnel projects 1 cm from the mantle and extends to about the level of the anterior margin of the eye. The funnel organ forms on each side a *V*-shaped swelling the

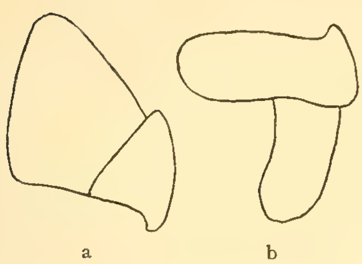


FIGURE 52. a upper jaw; b lower jaw of *Polypus valdiviae*.

FIGURE 53. *Polypus valdiviae*. Right half of a row of teeth of the radula.

outer arm of which is slightly shorter than the inner. The velar membrane is moderately wide and continues on the arms as a narrow fimbria which is of a varying length.

The 3rd right arm of the male is hectocotylized (Plate LXXX, Figures 3, 4). The velar membrane
486 continues ventrally to the proximal fold which projects outward at an acute angle and forms a groove. The spoon-shaped terminal part is bordered laterally by two large cheeks and between them are 5 large transverse swellings separated by deep grooves; the short, rounded tip is curved toward the cavity. Comparison with the hectocotylus of the two species mentioned above (*loc. cit.*, p. 324) shows similarities but also marked differences, so that these 3 species are easily distinguished.

Body and head are 2.5 cm wide; other measurements are as follows: dorsoventral diameter 1.9 cm; mantle length 3 cm; length of eye opening 6 mm; length of dorsal arms 6 cm; length of hectocotylus 5 cm.

The jaws (Figure 52) are large, with markedly curved tip. The radula (Figure 53) has broad median plates which are slightly concave anteriorly; the cutting edge narrows rapidly at first and is rather large, pointed, without lateral denticles. The inner intermediate plate is small, wider than long, with a very short, sharp edge; the outer intermediate plate is larger, with a very short edge toward the middle of the radula. The lateral plate is very large and slightly curved. The marginal plate is much wider than long.

Polypus levis (Hoyle)
(Plate LXXIX)

by Professor Dr. J. Thiele (Berlin)

1885 *Octopus levis*, Hoyle in: *Ann. Nat. Hist.*, ser. 5, Vol. 15, p. 229.
1886 *Octopus levis*, Hoyle in: *Rep. Voy. "Challenger"*, Vol. 16/I, p. 98, Plate 2, Figures 1–4; Plate 3, Figure 1.

Locality: Station 160: Port Gazelle, Kerguelen Islands.

The only specimen caught by the Deep-Sea Expedition, a male, is much larger than the *Challenger* specimens. The body is 75 mm long to the base of the arms, 40 mm thick and 60 mm wide; the head is 50 mm wide and the mantle is 55 mm long. The arms are of almost the same length; the dorsal arms are 160 mm long, the ventral arms 172 mm, the other two pairs 165 and 170 mm. The hectocotylized arm is 115 mm long and its terminal part measures 15 mm.

The South Pole Expedition collected also another species and its differences from *P. levis* will be described.

487 ## *Polypus granulatus* (Lamarck)

by Professor Dr. J. Thiele (Berlin)

A large female collected near Cape Town probably belongs to this widely distributed species. However, the statement that the ventral arms of this species are the longest is not correct as its ventral arms are only 19 cm long, while the other arms are 23 cm long. There are no other differences.

Polypus vulgaris (Lamarck)

A large specimen from the Great Fish Bay [Tigres Bay] probably belongs to this species.

Juvenile stages of *Polypus*

Polypus juv.
(Plate LXXVII, Figures 2, 7)

We shall begin the description of the young stages of *Polypus* (*Octopus*) with a juvenile specimen dredged in shallow water at Station 244 near Zanzibar. Its characteristic form is shown in Figure 2; the total length is 13 mm, the mantle being 6 mm long. Dorsal body length is 8.5 mm to the anterior margin of the eye.

The **arms** are thick and well developed but show no distinct differences in length. The mouth is surrounded by 8 small suckers which are surrounded by another circle of 8 much larger suckers. Several arms have a 3rd large sucker, followed by paired suckers which become gradually smaller to the tip. A wide, sail-like outer membrane connects the arms from the bases up to the proximal third of the suckers.

The **funnel** is moderately large and extends to about the level of the middle of the eye. Its closing apparatus shows some special characters. Examination from the ventral side under oblique

illumination shows that the free margin of the mantle differs from the other part of the mantle in being slightly cylindrical. Opening of the mantle cavity shows on each side a deep slit behind the projecting mantle margins which extends almost to the gills. The slightly curved posterior lateral margin of the funnel enters this slit, forming an effective closure.

The larva shows a more or less uniform pigmentation on the dorsal and ventral side of the mantle. The neck shows fewer chromatophores and the funnel is almost without chromatophores. Very large, deeply situated, symmetrically arranged chromatophores are indistinctly visible in the dorsal and ventral parts of the head. All arms bear two outer rows of chromatophores between which are situated isolated smaller ones, mainly at the tips. There are no chromatophores on the suckers. The species of the larva cannot be determined.

488

Polypus—**younger larva**

(Plate LXXVII, Figure 3)

The larva described above was collected in shallow water but the younger larva described here is pelagic. It was caught with a vertical net at Station 207, southwest of the Great Nicobar Island. It has a plump body with a sac-shaped mantle, relatively large eyes, and thick arms; the 3rd arms are slightly longer than the others. The closing apparatus of the funnel, especially the two lateral slits of the mantle, closely resembles that of the larva described above. The pigmentation is caused by dense chromatophores which are slightly more numerous on the ventral side than in the neck region. Three pairs of deeply situated large chromatophores are visible shining through at the level of the optic ganglia. The arms bear two rows of chromatophores and there is also one chromatophore on each sucker. The arms are connected by weakly developed outer membranes. Each arm bears two unpaired suckers at the base, of which those near the mouth are rather small. Distal to these suckers begins the normal pattern of paired suckers.

This larva probably belongs to *Octopus brevipes* D'ORBIGNY (*Céph. acét.*, Plate XVII, Figure 1/3).

Larvae of Octopoda covered with bristles

(Plate LXXVIII)

Seeing for the first time the form of a larva covered with bristles, such as is illustrated on Plate LXXVIII, Figures 2, 3, I was surprised, as such formations are rather unexpected in juvenile Cephalopoda. I found later that the larvae of *Octopus vulgaris* have similar tufts of bristles. However, a review of the literature showed that such bristles had already been observed by KÖLLIKER (1844, p. 164, Plate VI, Figure 64) in embryos of *Argonauta argo*. KÖLLIKER considered them at first as cilia, but he later found that they are not motile but are tufts of hairs which cover the head and mantle and are especially numerous in the vicinity of the eyes. I have already reported on such tufts in adult pelagic deep-sea Octopoda. These hairs apparently persist throughout life in these forms, while those found in the majority of Octopoda, especially those inhabiting shallow water, are characteristic for the embryos and newly hatched larvae and later disappear. In addition to this bristle garment, the larva shows the following characters:

The larva was caught with a vertical net, sunk to 1,300 m, at Station 41 in the Guinea Current,
489 and was only 5 mm long (see figure). Its sac-shaped mantle has a broad slit and its margin has become slightly detached from the funnel the lateral ventral margins of which are slightly folded up.

The relatively large **eyes** are typical for the Octopoda in that the lens projects from the circular lid. The arms (Figure 5) are still weakly developed, plump, and of about the same length. The spherical "anlagen" of the olfactory tubercles are visible shining through laterally at the points of attachment of the mantle.

The **pigmentation** is caused by large chromatophores which are more numerous on the ventral than on the dorsal side. Each eye is covered dorsally with 5 large chromatophores behind which is a larger chromatophore at the level of the attachment of the mantle. The arms bear chromatophores in 2 rows; there is also a large single chromatophore at the base. Examination from the ventral side shows two symmetrically arranged chromatophores on each side on and near the funnel. The funnel adductors are visible through the skin and end anteriorly near small, yellowish knobs of unknown function.

The tufts of bristles cover the dorsal and ventral side of the mantle, the funnel, eyes and neck to the base of the arms. The tufts are thin, stiff and arranged in oblique, crossing curves. All tufts are spread and apparently fully developed at this stage.

The tufts of bristles of a second larva (Plate LXXVIII, Figure 1) are apparently just about to break through to the outside. This larva was caught with a vertical net sunk to 1,900 m, at Station 223 in the South Equatorial Indian Countercurrent. It resembles the larva described above but is slightly older and is therefore more strongly pigmented. Regularly arranged chromatophores cover the dorsal and the ventral side of the mantle, those on the ventral side are more strongly pigmented; smaller, lighter-colored chromatophores are situated between the larger, dark-pink-colored chromatophores. The chromatophores on the funnel are less dense, and the superficial layer of chromatophores is almost absent on the ventral side of the head. Two median and four symmetrically arranged chromatophores are visible shining through on the dorsal side of the head, at the level of the optic ganglia. One pair of deeply situated chromatophores is present on the ventral side of the head at the base of the 4th arms, and one pair near the funnel. The arms bear 2 rows of chromatophores on the outer side, but there are no chromatophores on the suckers.

This specimen resembles the small larva described above in form, but it has a more cylindrical body and less protruding eyes. Around the mouth (Figure 4) is a ring of 8 small suckers, surrounded
490 by a second ring of 8 very large suckers. Then follows a third ring of 8 smaller suckers, and then biserial pairs of suckers, about 3 pairs on each arm.

The bristles begin to break through and form tufts, but the bristles have not yet spread.

Bolitaenidae CHUN

by Professor Dr. J. THIELE (Berlin)

CHUN established this family in the Promotion-Renunciation Program of the Faculty of Philosophy at the University of Leipzig (1911, p. 20). He defined it as follows: Octopoda with completely gelatinous body; cranial cartilage reduced to small rudiments; eyes widely separated, with long optic nerve; olfactory tubercle stalked; 3rd arms the largest; hectocotylization consisting in enlargement of all (*Bolitaena*) or only the distal (*Eledonella*) suckers of the 3rd right arm.

We add that the jaws are very soft and have a slightly curved cutting edge; the radula shows a marked widening of both pairs of plates near the median plate, making the entire radula very wide—a good character of the family.

Eledonella VERRILL

by Professor Dr. J. THIELE (Berlin)

CHUN (*loc. cit.*, p. 16) adds the following differences from *Bolitaena* to VERRILL's description of the genus (*Transact. Connecticut Acad.*, Vol. 6, p. 144): eyes relatively small and nearly spherical; optic nerve very long; arms delicate, semitransparent.

The hectocotylized arm has already been illustrated by VERRILL (*loc. cit.*, Plate 32, Figure 2). Since CHUN places *E. diaphana* in *Bolitaena*, he names the single species of the genus "*E. pygmaea* VERRILL". BERRY (*Proc. U.S. Mus.*, Vol. 40, p. 589, 1911) briefly described a Californian species as "*Eledonella healthi*" which, however, due to its very large eyes, probably belongs to *Bolitaena*; its hectocotylus is unknown.

Eledonella pygmaea VERRILL

(Plate LXXXI and Text Figures 54–56)

Locality: Station 53: 1°14.2′ N, 2°10′ W. Vertical net at 3,500 m. Gulf of Guinea.

The only female caught by the Deep-Sea Expedition is illustrated after the live animal on Plate LXXXI, Figure 5. The young specimens (Figures 1 and 2) were not found by the expedition; the male

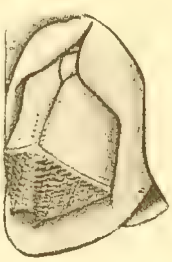


FIGURE 54. Pharynx of *Eledonella* after removal of the jaws.

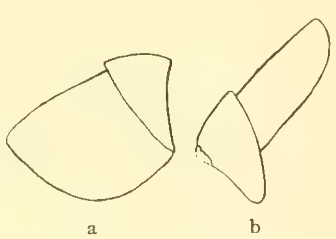


FIGURE 55. *Eledonella pygmaea*. a upper jaw; b lower jaw, lateral view.

in Figure 3 probably belongs to the material of the *Michael Sars* Expedition. Figure 4 shows the hectocotylized arm of what is probably a young specimen, of unknown origin.

491 The jaws of the specimen examined are shown in Text Figure 55. There is a structure resembling that of *Amphitretus* on the culting edge of the lower jaw. The jaws are very wide (Text Figure 54). The

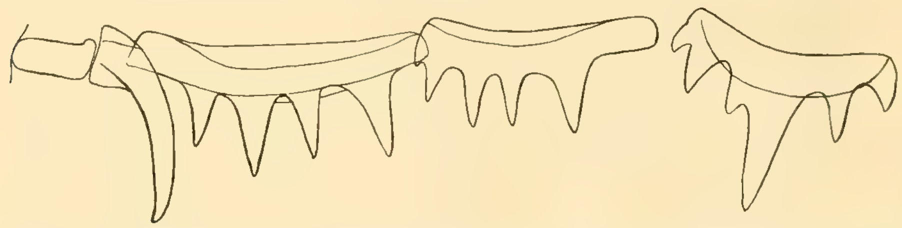


FIGURE 56. Radula of *Eledonella*. Left half of a row of teeth.

basis of the middle plate (Text Figure 56) is wide and anteriorly slightly concave; it bears a large median tooth—which often has a lateral process—and two smaller teeth on each side. The base of the inner intermediate plate is slightly wider than the median plate and has no teeth near the inner end; the inner tooth is the largest, the two following teeth are of about the same size, and the 4th tooth is distinctly smaller; there is a small denticle at the outer corner. The outer intermediate plate is wider still and has 4 pointed teeth of which the 1st and the 3rd one are larger than the other two. The lateral plate has a long, narrow, slightly curved cutting edge. The marginal plate is wider than long.

The funnel organ consists of an angular stripe 2.5–3 mm wide; its halves are directed obliquely posteriorly and form a right angle anteriorly.

Bolitaena (Steenstrup) Chun

by Professor Dr. J. Thiele (Berlin)

Chun (*loc. cit.*, p. 17) gives the following diagnosis of the genus: eyes elliptical, relatively large; arms strong, opaque in preserved specimens; all suckers of the hectocotylized 3rd right arm enlarged.

Hoyle named the only species of the genus *Bolitaena* "*microcotyla*" (Steenstr. MS). He noted (*Rep. Voy.* "*Challenger*", Vol. 16/1, p. 16) the reddish coloration, the wide opening of the mantle, the short arms which are connected by a membrane almost to the apex and bear a row of small suckers, and the very slightly curved jaws; he stressed that the rows of teeth of the radula recur regularly, each fifth row resembling the first one—a slightly ambiguous statement. Hoyle placed his species *diaphana* in *Eledonella* and not in *Bolitaena*. Surprisingly, Chun places this species in *Bolitaena* and also considers this species to be the type of the genus.

An examination of the type species of *Bolitaena* was therefore desirable. The Copenhagen Museum
492 kindly sent me two specimens so that I could complement the scanty data of Hoyle, but since both specimens were females, the structure of the hectocotylus could not be clarified.

The larger specimen is poorly preserved—it consists of a head without eyes, patched on to a sac-shaped posterior end. The ends of the arms are lost, so that the length of the arms cannot be determined; the 2nd arm is about 5 cm long. The suckers are small and widely separated. The small mouth is surrounded by a whitish ring about 1 cm wide. The armature of the pharynx resembles that of *B. diaphana*; the jaws are of similar form and the radula (Text Figure 57) shows only small differences, although there is a marked variation of the plates. Hoyle's statement is thus difficult to understand.

The smaller female is intact; it is 75 mm long from the posterior end to the end of the 2nd arm and has a very soft, gelatinous body. A web connects the larger proximal halves of the soft, translucent arms

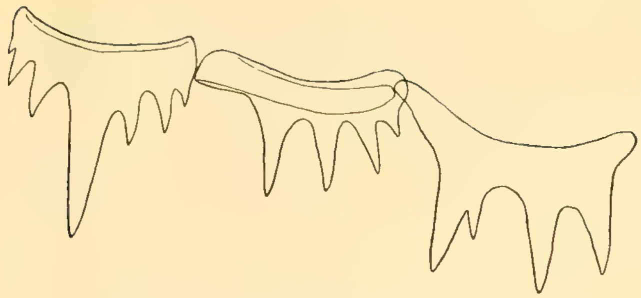


FIGURE 57. Median and intermediate plates of radula

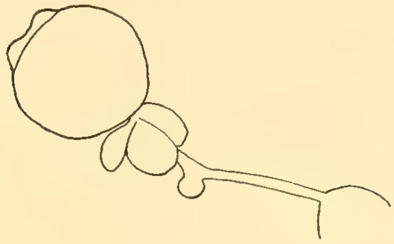


FIGURE 58. Optic nerve

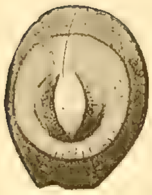


FIGURE 59. Eye

and its anterior side bears dark-brown radial stripes between the arms. The 2nd arms are the longest, slightly over 30 mm long; one of them bears 14 suckers, but a few suckers on the distal end may have been lost.

As CHUN paid special attention to the eyes and their nerves, I made preparations of them (Text Figure 58). The eye (Text Figure 59) is not very large, about 6.5 mm long (dorsoventrally) and 5 mm wide, i.e., nearly ovoid, though not as long as in *B. diaphana.* The nerve is long; the ganglion pedunculatum is situated close to the optic ganglion but the two ganglia are still distinctly separated. There is a median septum in the mantle cavity.

This species belongs therefore undoubtedly to the same genus as *diaphana.* The optic nerves are intermediate in length between *B. diaphana* and *Eledonella pygmaea.* The nerve becomes perhaps longer with age; at any rate, its length should be considered as a specific, not a generic character. The difference between hectocotylized arms, too, is possibly specific rather than generic; (unfortunately, nothing is known about the condition in *B. microcotyla*). If the difference is only specific, *Bolitaena* should be united with *Eledonella,* while *B. microcotyla* is intermediate between the other two species.

HOYLE's genus *Japetella* is distinguished by HOYLE mainly by the absence of a septum in the middle of the branchial cavity.

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Bolitaena diaphana (HOYLE)

(Plates LXXXII–LXXXIV and Text Figures 60 and 61)

Locality: Station 44: 5°5.3′ N, 13°27.5′ W. Vertical net, 3,070 m. South of Sierra Leone.
Station 50: 0°26.3′ N, 6°32′ W. Vertical net, 4,000 m. Gulf of Guinea.
Station 54: 1°51′ N, 0°31.2′ E. Vertical net, 2,000 m. Gulf of Guinea.
Station 55: 2°36.5′ N, 3°27.5′ E. Vertical net, 1,200 m. Gulf of Guinea.
Station 64: 0°25.8′ N, 7°0.3′ E. Vertical net, 2,200 m. Gulf of Guinea.
Station 65: 1°56.7′ S, 7°40.6′ E. Vertical net, 2,400 m. Northeast of S. Thomé.
Station 66b: 3°55′ S, 7°48.5′ E.
Station 182: 10°8.2′ S, 97°14.9′ E. Vertical net 2,400 m. Indian South Equatorial Current.
Station 190: 0°58.2′ S, 99°43.2′ E. Vertical net, 1,100 m. Near Sumatra.
Station 217: 4°56′ N, 78°15.3′ E. Vertical net, 2,000 m. Southwest of Ceylon.
Station 231: 3°24.6′ S, 58°38.1′ E. Vertical net, 2,000 m.
Station 232: 3°26.2′ S, 58°34.2′ E. Vertical net, 1,500 m. East of the Seychelles.

This species was described from the Pacific Ocean (0°42′ S, 147° E), and later by CHUN (*Report "Michael Sars" Exped.,* Vol. 3, Part 1, p. 20) from the Atlantic; according to these records and those of the Deep-Sea Expedition, it is widely distributed in warm seas.

Several specimens are illustrated on Plates LXXXII and LXXXIII. The specimen in Figure 1 of Plate LXXXII is from Station 66b; Figures 2 and 3 are of a small specimen from Station 50; Figure 4 shows the anterior side of the arms and the pharynx of a larger male (Station 66b?); Figure 1 of Plate LXXXIII shows a small specimen, 25 mm long, from Station 190, Figure 2 shows a similar specimen (about 18 mm long) from Station 217, Figure 6 the arms of the same specimen, Figures 3 and 4 as well as Figure 5 a specimen (about 3 cm long) from Station 44, Figures 9 and 10 an eye of the animal from Station 65.

The buccal armature closely resembles that of *Eledonella pygmaea* but the intermediate plates of the radula are not so markedly widened. The median plate (Text Figure 60) has 3 shorter teeth lateral to the large median tooth; the inner intermediate plate is markedly narrower than the median plate and has 4 teeth. The lateral and marginal plates resemble those in the other species. The anterior median plate is shown above the other plates so as to illustrate the marked enlargement posteriorly.

494 Text Figure 61 shows the outline of the funnel organ: it is right-angled anteriorly, slightly concave posteriorly, with short lateral parts.

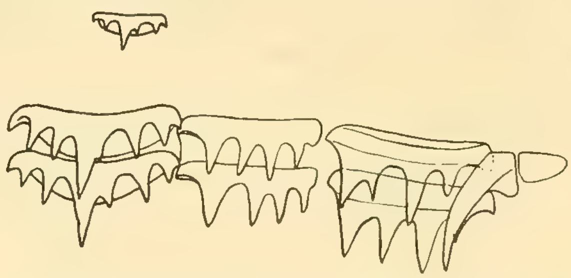

FIGURE 60. Radula of *Bolitaena diaphana*. Part of posterior half of radula: above it, the anterior median plate.

FIGURE 61
Funnel organ of *Bolitaena*.

CHUN indicates in his notes the following measurements for the specimen from Station 66b:

Right 1st arm (including margin of lip)	38 mm,	left 35 mm;
Right 2nd arm (including margin of lip)	41 mm,	left 42 mm;
Right 3rd arm (starting from margin of lip)	51 mm,	left 55 mm;
Right 4th arm (starting from margin of lip)	42 mm,	left 42 mm.

The membrane between the 1st arms and between the 1st and 2nd arms extends to half the length of the arms; that between the 2nd and 3rd arms extends as far as 16 mm, i.e., nearly a third of the length of the arm; between the 3rd and the 4th arm it reaches as far as 18 mm of the 4th arm, i.e. over a third of its length; the membrane between the 4th arms is weakly developed.

The hectocotylus bears 4 suckers at the base; the 5th–11th (or 12th) suckers are larger, and the following ones smaller, up to the 21st sucker which is very small. The left 3rd arm also bears 21 suckers. The mantle is about 50 mm long.

Anatomy of *Bolitaena* and *Eledonella*

by Professor C. CHUN

1. Structure of mantle

The gelatinous texture of the body of *Bolitaena* is particularly marked in the mantle. Interesting is, on the one hand, the adaptation of the mantle to the gelatinous swellings, inviting comparison

with the robust mantle of other Octopoda, and on the other hand, the fine structure of the nervous system and of the chromatophores which is far better recognizable through the transparent gelatinous tissue than it is in other Cephalopoda. I described the structure of the mantle and especially the chromatophores of *Bolitaena* in an earlier communication (*Verh. Deut. Zool. Ges.*, 1902), but it is desirable to review the previous observations in the light of recent re-examination.

The mantle consists of the following layers:

1. Outer epithelial layer.
2. Gelatinous cutis with chromatophores.
3. Three outer muscular layers.
4. Gelatinous tissue of the mantle with radially arranged bands of muscles.
5. Inner muscle layers (facing the respiratory cavity).
6. Inner epithelium.

The outer epithelium was damaged in all specimens: in the few places where it is preserved, it consists of markedly flattened, oblong cells many of which contain numerous granules.

The peculiar tufts of bristles are also derived from the ectoderm. In *Bolitaena* they persist for a
495 long time, while in other Octopoda they are present only during the youngest larval stages. The abundant development of these tufts has already been described and illustrated for the young stages of *Argonauta*. The tufts were first observed by Kölliker (*Entwicklungsgeschichte der Cephalopoden*, 1844, p. 164 and Plate VI, Figure 64) who described them as follows:

> "The peculiar cover of the mantle was found only in older embryos and consisted of tufts of fine hairs scattered over the whole body, on head and mantle, but most numerous near the eyes. I never observed movements; the hairs of each tuft remained closely stuck together. Detached tufts were often found in the water near the embryos: each tuft was inserted on the plane side of a hemispherical cell that measured 0.006‴ in diameter and contained only a light-colored fluid. These hairs were not motile either, did, however, not always stick together but often spread like a brush, probably due to mechanical factors."

Similar tufts of hairs were later observed by Joubin (1893) on the stalk of the suckers of *Chiroteuthis*. Joubin, however, failed to recognize that he, too, was dealing with the earliest stages of development of these peculiar formations when he began to examine the development of the chromatophores. This is why he considered the early stages of the hair tufts to be the first "anlagen" of chromatophores and assumed that each chromatophore developed from an enlarged basal cell which belongs to one of the solid clusters of cells which had become deeply embedded. He thought that mesodermal cells become radially arranged around the basal cell and later develop into the radial muscle fibers.

It will be shown below that the development of chromatophores takes an altogether different path. We note here only that the solid, deeply situated ectodermal processes are the "anlagen" of the tufts of bristles, which are often present in large numbers in embryos of Octopoda. In the embryos of *Octopus* they are scattered over the whole body and are so densely developed on the arms that it is difficult to understand that later embryologists did not notice them. They are oval groups of cells (Plate LXXXIX, Figure 10) with a larger basal cell which is at first surrounded by smaller cells.

Inside the group is situated a strongly refractile, finely striated cone which consists of a homogeneous substance. Joubin apparently observed this formation, as his drawings show a fine striation of the inner cavity. These stages are the precursor of the tufts of bristles: the plug of ectodermal cells gradually flattens and the smaller peripheral cells slightly shrink while the apex of the striated cone appears on the outside and splits into a tuft of thin chitinous bristles (Figures 11, 12). The bristles are situated on a cuplike chitinous base (Figure 13) at the margin of which often extend fibers which resemble

the muscular processes of young chromatophores, as will be described below. I assume that these are radial muscles which upon contraction cause the delicate tuft to spread.

496 I am no more able than Kölliker to explain the physiological significance of the tufts. They are not sense organs because of the absence of a nerve supply and because the tuft is inserted on a relatively thick chitinous base. In view of the large number of these tufts on the body and arms of freshly hatched embryos of *Octopus*, one may assume that small food objects become mechanically entangled in them.

Still more difficult is the phylogenetic interpretation of the formation. The hair tufts are epecially characteristic for the larvae of the higher Cephalopoda, the Octopoda; they are absent in the Decapoda or play only a minor role. Is this a reminiscence of a bristly ancestor of the Cephalopoda? Though this would, indeed, be an attractive proposal, the more so as the development of these tufts markedly resembles that of the brushes of oligochaetes, it is too speculative to be further pursued.

Cutis. The subcutaneous connective tissue forms a gelatinous layer the basis of which is formed by small cells of connective tissue which branch and divide into long, fine fibers. These cells are relatively sparse and are often overlooked because they are covered by other elements of connective tissue, i.e. the developing chromatophores of the young animal.

Even more difficult to recognize is a layer of flattened, almost endothelium-like cells of connective tissue situated directly on the musculature and having nuclei of irregular or branched form. Some of these nuclei are situated between the muscle fibers and are intensively stained if seen from the narrow side. The coloration will be described in detail in connection with the structure of the chromatophores. For the present we note only that the gelatinous cutis contains not only numerous chromatophores but also blood vessels and a rich network of nerves; it also forms the superficial muscular layer, which is of special interest and will be described in detail.

Outer musculature of the mantle

The outer musculature of the mantle consists of three layers of which the deepest layer, the one facing the gelatinous tissue, is much thicker than the other two and consists of circular muscles. On this layer is situated a thin layer of longitudinal fibers; this is followed by another layer that is still partly embedded in the cutis and consists of branched transverse and longitudinal fibers.

Examination of a young specimen of *Bolitaena* preserved in Flemming's solution (this descrip-
497 tion is based on the specimen from Station 190) shows a system of fibers that are somewhat blackish, due due to the influence of osmic acid. These fibers radiate from the posterior end of the body and extend to the mantle margin. The longitudinal fibers are crossed at right angles by transverse fibers, so that square or rectangular fields are formed. The system of crossing fibers is not strictly regular; as shown in Figure 9 of Plate LXXXIX, some fibers are thick and branched, others become united. This fibrous system is of interest because the larger chromatophores are connected with it (Figure 9). The arrangement of chromatophores in rows is present not only on the ventral but also on the dorsal side, at some points of which it is even more distinct.

Microscopic examination of the skin (Plate LXXXIX, Figures 1, 2, 3) shows a delicate network of smooth muscles; in young specimens only the thicker longitudinal or transverse cords are visible under the magnifying lens. These cords show a fine longitudinal striation caused by densely arranged smooth contractile fibers with elongate nuclei. The striation sometimes disappears at the periphery of the fibrous systems, where it is replaced by a rich branching. Some thicker lateral branches radiate fan-like from the main branch and are again finely striated, other branches are thinner and have no muscle fibers. The branching is sometimes so dense that a fine network with numerous anastomoses

is formed. This ramification is most marked at the ventral margin of the mantle. Here the thicker longitudinal or oblique cords often radiate like a fan or, rather, like a veritable thicket of fibers (Figure 2). This network of anastomosing fibers is not restricted to the mantle margin. The thicker cords have lateral branches which form a fine network with thickened knots on which the striation caused by the muscle fibers is not recognizable. If it were not for the distinct connection with thicker muscle cords, this network could easily be considered as connective tissue.

Gelatinous tissue of the mantle

The gelatinous tissue of the mantle is much thicker than are the outer and inner muscular layers. In larger specimens the gelatinous layer is nearly 10 mm thick. It consists of numerous thin fibers which cross each other in various directions. Even under high magnification I did not find swellings on these fibers—which have double contours—that could be interpreted as a nucleus or as a cell body. They are apparently elastic fibers that have crystallized out of the soft gelatinous mass, in a manner similar
498 to that of the connective tissue of vertebrates. However, these fibers are certainly not connected with the relatively large cells of connective tissue that are sparsely scattered present in the gelatinous tissue. These cells are of irregular form and are apparently able to make ameboid movements. Some of them are rounded, others have broad, lobed pseudopodia, and only a few have long, thin processes. The nuclei of these cells are spherical and homogeneous, while the surrounding protoplasma is more or less granular.

Some cells have a light-colored vacuole. Others have two nuclei and are obviously dividing, which is also evident from the shape of the two nuclei: they resemble a "ladyfinger" biscuit. I did not discover a connection between these cells and the gelatinous fibers. In cleared, alcohol-preserved material, in which the contours of the cells and the gelatinous fibers are sharply visible, one can clearly see that the fibers and cells are independent.

The gelatinous substance contains capillaries and a few nerves that are less branched than the capillaries and the nervous network of the cutis.

Other distinct formations in the gelatinous substance are the radial muscular bands. These are as long as the gelatinous substance is thick, and their width is 0.23 mm in the largest specimen. The broad side of the bands is always perpendicular to the longitudinal axis of the body. A cross section of the mantle shows the broad side of the bands, a longitudinal section shows their sharp edge. The bands consist of a single layer of smooth fibers which contain long nuclei. The bands divide into fibers at their insertion in the outer and inner musculature. The larger processes sometimes branch and show a fibrous structure caused by radiating musculature.

Inner musculature of the mantle

The inner musculature of the mantle consists of two layers, a thin layer of longitudinal fibers bordering on the gelatinous substance and a thicker layer of circular fibers which is covered with the epithelium of the mantle cavity; on the weakly developed, widely spaced longitudinal muscles are situated branched nuclei resembling those mentioned in connection with the cutis.

The gelatinous condition has caused important modifications. The outer and inner layers of circular muscles are broadly separated by the thick gelatinous tissue and they are too weakly developed to be capable of strong action. The radial muscles in the mantle of Cephalopoda are divided into separate muscular bands, and the longitudinal musculature is very weakly developed. The gelatinous

condition of the mantle affects also the cutis, so that its fine structure becomes more clearly recognizable.
499 The branched musculature of the deeper cutis and the well-developed plexus are more distinct in *Bolitaena* than in all other Cephalopoda.

2. Mantle complex

(Plate LXXXIII, Figure 5; Plate LXXXIV)

Opening of the mantle cavity shows the entire funnel, which is moderately large and projects with its lip-shaped opening to about the level of the middle of the eye (Plate LXXXIII, Figure 5; Plate LXXXIV, Figure 1). The funnel is fused laterally with the gelatinous tissue of the body, and its adductors are not visible from the outside. The deeply concave posterior margin of the funnel ends in a thin lamella and passes gradually into the depressors.

Opening of the funnel shows that there is only a single dorsal funnel organ (Plate LXXXIV, Figure 3, *org. inf.*). It is roof-shaped and has two broadly diverging arms. However, I assume that the apparently unified structure is secondary and caused by the fusion of the paired lateral ventral parts with the dorsal part. The cream-colored organ stands out distinctly over its light-gray surroundings.

If the mantle septum is preserved intact during the opening of the mantle cavity, it appears that the septum (*sept*) is formed by the very strong median mantle retractor; the latter is situated broadly on the abdominal wall, becomes narrower toward its insertion in the mantle, and then radiates like a fan anteriorly and posteriorly.

The muscle contains a gelatinous substance that is situated on the contractile fibers which extend antero-posteriorly. The gelatinous substance also contains branches of the veins of the septum; the branches open into the vena cava. Thicker branches of the artery of the septum are also visible.

The musculus collaris, which is inserted dorsally on the mantle behind the eyes and leaves a free band 11–12 mm wide on the dorsum, originates on the lateral walls of the funnel.

The funnel depressor is delicate. It is situated on the lateral ventral parts of the abdominal wall, tapers posteriorly and projects only slightly beyond the mantle ganglion on each side.

The lateral mantle adductor originates in the form of a band dorsal to the funnel depressor and widens like a wing posteriorly toward the mantle. Its ventral side borders on the pallial nerve and the stellate ganglion; dorsally from the latter it radiates into the mantle. It is not divided into an anterior and a posterior part. The stellate ganglion has 7 large branches on the left side and 9 on the right side in the largest specimen. The muscle widens like a fan from the mantle toward the lateral walls of the body and its curved margin does not reach the funnel depressor in the middle.

The vsiceral sac is strongly pigmented dorsally and ventrally by large purple chromatophores (Figure 1). In most specimens, only the branchial hearts, gills and oviducts are not pigmented. The envelope of chromatophores extends between the renal sacs, ovary and oviducts, and covers also the
500 dorsally adjacent parts of the intestine, i.e., esophagus, crop and stomach. The pigmentation of the male genitalia will be discussed later.

The branchial hearts are relatively large and situated close together. The gills have 6 wrinkled lamellae of which the outer ones are at least twice as large as the inner ones. The suspensorium extending from the branchial gland is wing-shaped and markedly drawn-out anteriorly, the pallial vein extends on its posterior margin.

In the large female examined, a ligament extends proximal to the dorsal crest of the gill and

surrounds the oviducts, forming a pocket from which project the openings of the oviduct gland. This lamella covers the renal opening the chimney-shaped papilla of which adheres to the oviduct.

Deeper parts of the abdominal wall

The topography of the deeper parts, situated below the funnel, is here described because some parts which are clearly visible in other Octopoda are not visible from the outside in the gelatinous Bolitaenidae. This region has complicated relationships with the deeply situated organs, i.e., the static organs and the nerves which originate in the brain.

If the funnel is separated from the abdominal wall at the concrescence on the right side and is folded aside, the funnel adductors are visible. There are two pairs: the lateral and the median adductors. In the largest specimen from Station 66 the median adductor is much narrower than the lateral adductors. The median adductor originates on the inner (ventral) margin of the 4th arms and diverges toward the median dorsal surface of the funnel, passing around the funnel nerves and the vena cava; the latter shines through. The lateral adductor extends broadly toward the dorsal lateral wall of the funnel, tapers slightly, passes ventrally over the ring of the arm vein, turns toward the dorsal side of the base of the 4th arm, and disappears dorsal to the arm vein. This muscle, and the others described below, has a silky sheen in the preserved specimen.

A large triangular muscle extends from the posterior base of the 4th arm and tapers rapidly toward the outer side of the lateral adductor of the funnel. This conical muscle, which is filled with gelatinous tissue, may be considered as the extended base of the ventral arms.

There are also some smaller muscles which are more distinctly differentiated from the muscular cover only in older specimens. One of them is a thin muscle which extends divergently between the median adductors of the funnel. Another muscle extends obliquely between the median adductors and the triangular muscle. There is also a horizontal muscle; it begins at the level of the passage of the olfactory nerve through the muscular lamella and extends almost to the middle of the dorsal wall of the funnel.

501 The fusion of the funnel adductors with the triangular muscle and the small horizontal muscle forms a muscular lamella which is situated on the thin muscular lamella of the ventral abdominal wall and is fused with it along a concave curve behind the orbit. This thick outer muscular lamella can be detached by a cut from the thinner, more deeply situated lamella. This envelope, which is formed by the fusion of the above muscles, serves for the insertion of the inner margin of the collaris; it is fused posteriorly with the thick musculature of the abdominal wall on which the lateral adductor, the funnel depressor and the musculature of the septum are inserted.

That this thick muscular lamella can have passed only secondarily over the thin, more deeply situated musculature of the abdominal wall is proved by the presence of chromatophores. Removal of the outer muscular lamella shows large chromatophores situated on the thin inner muscular lamella. Where free chromatophores are visible in preserved specimens, e.g., on the posterior abdominal wall, at both sides of the septum, at the level of the liver, the genitalia and the branchial hearts, this is due to the absence of a thicker overlying muscular lamella. The outer muscular lamella has a deep median indentation which extends far posteriorly, to near the anus, so that the thin underlying muscular lamella of the abdominal integument which covers the lateral parts of the static capsules becomes visible.

Veins. The two arms of the vena cava and their sac-shaped confluence into the single vena cava are visible in this area. The arms of the vena cava receive the veins of the arms which branch along the

arms. More distinct are the two branches of the vein for the 4th arm; one of the branches passes along the dorsal side of the 4th arm, the other one along the ventral side of the 3rd arm. Into the confluence of the arms of the vena cava opens the large ophthalmic vein and a smaller vein which passes to the posterior margin of the eye. The vein of the funnel also opens into the confluence of the arms of the vena cava.

The posterior nerves of the funnel pass anteriorly over the beginning of the vena cava, and the anterior nerves of the funnel are situated behind them. The posterior nerves innervate the lateral parts of the funnel, the anterior nerves its median parts. Deeper preparation shows the nerves of the adductors in front of the anterior nerves of the funnel which divide and innervate the inner and outer adductors.

The shining capsule of the statocysts is situated deeply. It is oval, its position is horizontal, and it has a median septum which separates the static organs. The capsule is covered, except for its median part, with the thin deeper muscular lamella; the latter extends to the margin of the triangular muscle.

502 3. Nervous system

(Plate LXXXV)

A cartilaginous capsule of the cranium is absent in this gelatinous form, which has instead a very thin, transparent envelope; I therefore expected that the nervous system would be distinctly visible. This was indeed the case, but there were difficulties because the specimen (from Station 50) was very small; it has a mantle length of about 38 mm. I added some details from a slightly larger specimen from Station 53 and from a smaller one from Station 49. The preparation of the nerves was very laborious because they are very thin. The fine nerves, especially the olfactory nerve, presented particular difficulty.

Central nervous system

The structure of the central nervous system is typical for the Octopoda. The ganglionic centers are situated closely together; particularly close is the adherence of the supraesophageal to the cerebral ganglion. However, there are shallow grooves which separate them and similarly separate the brachial ganglia from the large adjacent ganglionic swellings.

Cerebral ganglion (Plate LXXXV, Figure 1). The dorsally situated cerebral ganglion is about twice as wide as long; in dorsal view it is well delimited from the ventral ganglia because it is displaced relatively far anteriorly and situated on organs which pass through the brain. The anterior margin of the cerebral ganglion bears 3 tubercle-shaped swellings, one median and two lateral ones, which form a sharp boundary toward the supraesophageal ganglion (*g. bucc. s*). The cerebral ganglion is broadly fused laterally with the pedal ganglion (Figure 2, *g. ped*) below the base of the optic nerve, while its median posterior margin is situated on the complex of organs which lie in the canal between the cerebral and pedal ganglia: the esophagus, the salivary duct, the buccal arteries and the sympathetic nerves.

Pedal ganglion (Figure 2, *g. ped*). The ventrally situated pedal ganglion is only indistinctly differentiated from the visceral ganglion (*g. visc*). Examination from the ventral side shows a shallow groove which separates the two ganglia. The wide pedal ganglion projects posteriorly beyond the cerebral ganglion.

The **visceral ganglion** (*g. visc*) is heart-shaped, with truncate posterior apex and with a spherical, dorsally convex surface.

The **brachial ganglion** (*g. brach*) is separated from the pedal ganglion by a distinct constriction; it, too, is wide and relatively short. Its anterior margin is slightly concave between the origin of the arm nerves.

There is a special character of the brachial ganglion which has not been described so far. Prepara-
503 tion of the brain of *Eledonella pygmaea* from Station 53 showed a commissure which connects dorsally the two halves of the brachial ganglion (Figure 8, *c. brach*). This commissure branches from the almost equally wide brachio-buccal commissure (Figure 8, *c. brach. b*) and curves dorsally around the esophagus. Once alerted to this condition, I found it also in the smaller *Bolitaena* from Station 50. A median longitudinal cut through the supraesophageal ganglion (Figure 1, *g. bucc. sup*) shows that the brachial commissure has no connection with the supraesophageal ganglion but forms an independent and not-ramifying dorsal connection of the anterior lateral halves of the brachial ganglion.

The **supraesophageal ganglion** (Figure 1, *g. bucc. sup*) is broadly fused with the anterior margin of the cerebral ganglion but is sharply delimited from the 3 spherical swellings. It forms a half-ring, which is slightly narrower than the underlying brachial ganglion (*g. brach*). The supraesophageal ganglion has a thick commissure on each side which extends obliquely anteriorly to the brachial ganglion (Figure 8, *c. brach. b*) and leaves a spindle-shaped gap between the cerebral and the pedal ganglion. This commissure borders anteriorly on the brachial commissure.

The **infraesophageal ganglion** (Figure 1, *g. bucc. i*) is crescent-shaped. Its anterior margin borders on the anterior salivary glands which are situated on the ventral side of the esophagus. Its halves are not separated as stated by Meyer for *Opisthoteuthis* but are fused broadly in the middle. In *Eledonella pygmaea* (Station 53), the posterior margin is deeply indented and long commissures extend from it laterally to the supraesophageal ganglion (Figure 8, *c. b. s. i*).

Cerebral nerves

Nerves of the cerebral ganglion

1. The optic nerve (Figures 1, 2) is very long and, in contrast to other Octopoda (*Cirroteuthis*), extends to the optic ganglion (*g. opt*). This condition is mainly caused by the wide separation of the moderately large—i.e., relatively to the wide head—small eyes. This is most marked in *Eledonella pygmaea* which has the smallest eyes (Figure 8, *opt*). The optic nerve of this species is 7 mm long or nearly twice as long as the width of the brain, which is 4 mm wide. In the large male *Bolitaena* from Station 66, this nerve is shorter, i.e., as long as the brain is wide. The optic nerve is much shorter in juvenile specimens, the eyes of which are situated closely together, so that their shortened optic nerve is reminiscent of that of other Octopoda. It is, however, never as short as it is in *Eledone*. The optic nerve is accompanied by a branch of the ophthalmic artery—the arteria nervi optici—which arrives at the nerve posteriorly, some distance from its base. The optic nerve forms distally two ganglia: the ganglion pedunculi (*g. pedunc*) and the optic ganglion (*g. opt*). Klemensiewicz (1879, p. 32) proves that stimulation of the ganglion pedunculi causes total expansion of chromatophores of the entire body. Although these experiments were never repeated, his data were accepted by the physiologists. The ganglion pedunculi of *Bolitaena* and *Eledonella* is well developed (according to Meyer, 1906, p. 246, it is absent in *Opisthoteuthis*). This fact may be connected with the large number of chromatophores on
504 the surface of the body and in the visceral mass of this species. In *Bolitaena* (Figures 1, 2), the spherical ganglion pedunculi adheres closely to the optic ganglion (Station 53, Figure 8, *g. pedunc*), while in *Eledonella* (Station 53, Figure 8, *g. pedunc*) it is situated at the distal third of the optic nerve, i.e. far from the optic ganglion. This is a distinct difference between the two genera. In the area of the ganglion

pedunculi the optic nerve is slightly swollen and forms a bean-shaped ganglionic elevation (Figure 8, g^{1}) which is fused with the spherical chromatophore ganglion. In the fresh specimen of *Eledonella* from Station 53, this ganglion was yellowish and visible showing through.

The optic ganglion is dish-shaped, 2.5–3 mm in diameter in the large specimens, with a kidney-shaped constriction on the dorsal side.

2. The posterior ophthalmic nerve (Figures 1, 2, 7, 8, *n. ophth. p*) is thin, originates immediately behind the optic nerve and extends to the dorsal side of the eye. It is relatively thin because the eyes are relatively small. MAGNUS and JATTA described a nerve which causes the contraction of the pupil, whether that nerve is identical with the one described here is difficult to decide, in view of their incomplete description.

3. The anterior ophthalmic nerve (Figures 1, 7, 8, *n. ophth. a*) is thin, originates immediately in front of the optic nerve, and accompanies it dorsally for some distance. This nerve may be identical with the nerve that causes the dilatation of the pupil according to MAGNUS and JATTA. At half the length of the optic nerve and proximal to the ganglion pedunculi, the anterior ophthalmic nerve turns toward the ophthalmic artery and extends along it; here it is situated dorsal to the optic nerve.

4. The anterior nerve (Figure 8, *n. ant.*) is thin and originates on the dorsal anterior margin of the brain near the buccal ganglion. Again, it is difficult to decide whether this nerve is identical with the coloration (chromatophore) nerve of MAGNUS and JATTA.

Nerves of the pedal ganglion

On the pedal ganglion originate 6 nerves: 2 laterally and 4 from the lower side.

1. Olfactory nerve (Figures 1, 2, 7, 8, *n. olf*). I prepared this nerve in two specimens from the olfactory tubercle to the point where it leaves the central system. The olfactory nerve of *Bolitaena* certainly belongs to the cerebral ganglion. W. MEYER (1908, p. 246) states that in *Opisthoteuthis* this nerve is displaced to almost the esophageal ganglion.

The olfactory nerve undoubtedly serves mixed functions. Its greater part is strictly motoric, while the true olfactory nerve is a very thin branch the course of which to the olfactory tubercle will be described in detail.

The motor part is apparently homologous to the posterior oculomotor nerve described by HILLIG in agreement with ZERNOFF (1869). According to HILLIG, the two nerves are closely connected and separate only late. The posterior oculomotor nerve innervates the musculature of the eye on the ventral side of the orbit.

The olfactory nerve is moderately large, originates on the anterior lateral margin of the pedal ganglion, extends obliquely posteriorly, and then divides into a thin sensory nerve and a thick motor branch (Figure 2). This branch curves posteriorly and follows the musculature of the ventral part of the abdominal wall, extending for some distance at the border between the static capsule and the abdominal wall. I prepared the sensory nerve—starting from the olfactory tubercle and advancing posterior-
505 ly—in a younger specimen of *Bolitaena* (Station 49) and in the larger male from Station 66. It is visible through the stalk of the olfactory organ; after its exit, it ascends steeply anteriorly and curves over the margin of the collaris. It then extends to the posterior margin of the eyeball, passing close to the vein which extends to it, and then winds slightly and turns posteriorly toward the middle in the gelatinous tissue of the lateral ventral cover of the head. It then reaches a narrow muscle which extends from the mantle to the base of the lateral adductor of the funnel. Here the nerve passes through the gelatinous tissue that lies underneath the muscular lamella behind the optic ganglion, before reaching the muscle that extends obliquely posteriorly from the eye. It passes close to the ganglion pedunculi

and then curves slightly posteriorly and continues toward the main motor branch with which it eventually unites.

The olfactory nerve has thus undoubtedly a mixed nature: it has mainly motor functions but it also has a specific sensory branch to the olfactory organ. I already noted this double nature of the olfactory nerve in the Oegopsida, especially in *Chiroteuthis.* This condition is strange but it does not stand isolated. For example, the facialis of fishes and Perennibranchiata contains sensory branches to the lateral organs of the head, and motor branches to the musculature.

2. Accessory olfactory nerve (Figures 1, 7, 8, *n.acc.olf*). Close to the olfactory nerve of older specimens originates a nerve which, too, innervates the musculature of the abdominal wall. This nerve is separated from the olfactory nerve only in *Eledonella* (Figures 7, 8), while it forms a lateral branch of the olfactory nerve in *Bolitaena.*

3. Inferior ophthalmic nerve (*n. ophth. i*). This nerve is slightly thinner than the olfactory nerve and originates behind it from the lateral wall of the pedal ganglion. It then accompanies the orbital artery, curves obliquely posteriorly and continues for some distance straight; then it passes through the muscular lamella. It borders on a small ganglion on its dorsal side at the point where it passes through the lamella. It has a slightly winding course before innervating the lateral musculature of the abdominal wall, close behind the eye.

Chéron (1866, p. 26) also mentions the small ganglion situated in *Eledone* near the inferior ophthalmic nerve, but no mention of it is made by later authors.

4. Inferior oculomotor nerve (Figures 1, 2, 7, 8, *n.oc.i*). This is one of the thinnest nerves that originate on the lower side of the pedal ganglion. It originates on the lateral lower side of the pedal ganglion immediately anterior to the static nerve and extends toward the broad triangular muscle of the abdominal wall, dorsally to the ophthalmic vein. I do not know whether this nerve has further branches to the eye.

506 **5. Adductor nerve of the funnel** (*n.add.inf*). It originates as a paired nerve from the abdominal wall, directly anterior to the anterior funnel nerve (*n.inf.a*). In the large *Bolitaena* from Station 66 I found it ascending obliquely anteriorly around the static capsule, pervading the remnant of the cartilage-like cranial mass, and appearing behind the ophthalmic vein. Next it extends over the thin inner muscular lamella and divides on each side into a lateral and median branch for the funnel adductors.

6. N. staticus (*stat*[1], *stat*[2], *stat*[3]). In the past, this nerve was named the auditory nerve. Nobody mentioned that it is divided into 3 parts. The roots of this nerve converge near their exit from the brain, on the lateral lower side of the pedal ganglion. I could not determine whether these roots unite inside the ganglion into a common cord, but this is probable. Of the 3 branches, a short, thick branch extends obliquely medially to the pad of the statoliths, a longer branch extends obliquely outward and anteriorly to the crista statica which it reaches some distance behind its beginning, and the third branch extends posteriorly to the distal end of the crista.

I found these 3 branches in all static organs that I examined, so that it is certain that the nerve is divided into 3 branches. Previous observers stated that it is divided into only 2 branches.

7. Anterior funnel nerve (*n.inf.a*). This nerve originates at the border between the pedal and visceral ganglion, at the point where the brachial artery leaves the lower side of the pedal ganglion. The brachial artery has an arterial branch along each side of the funnel nerve. The two anterior funnel nerves are thick and extend toward the funnel between the two static capsules. They appear behind the confluence of the anterior vena cava, at the point where the ophthalmic vein opens into it, then extend near the sac-shaped swelling of the vena cava, and finally ramify to feed the lateral funnel bulbs.

Nerves of the visceral ganglion

Five nerves originate on the visceral ganglion (*g. visc*). The posterior nerves are so strongly compressed by the large static organs that they become united at the base and appear singly.

1. Posterior nerve of the funnel (*n. inf. p*). This nerve originates on the median posterior side of the visceral ganglion. In *Eledonella* it is compressed by the static organs into a single nerve which divides only later (Figure 7, *n. inf. p*). The nerve is thick, originates directly exterior to the visceral nerve (*n. visc*), and forms a curve at the anterior margin of the plane of contact between the two envelopes of the statocysts. In front of the confluence of the arms of the vena cava it turns toward the funnel and immediately after it, it divides, forming also a number of thinner branches. I found in the large *Bolitaena* from Station 66 that the two branches cross each other, forming a kind of chiasma. Each of these branches divides into 3 thick branches which innervate the median parts of the funnel.

The posterior nerve of the funnel has always been described as paired, because the static organs are relatively small and do not influence it so strongly as in *Eledonella.*

507 **2. Nerve of the vena cava.** This thin, single nerve originates closely anterior to the posterior nerve of the funnel and continues to the vena cava singly, notwithstanding the branching of the funnel nerve. This was distinct in sections through the distal part of the funnel nerve.

3. Pallial nerve (*n. pall*). The mantle nerves originate paired on the posterior lateral margin of the visceral ganglion, closely behind the inferior ophthalmic nerve (*n. ophth. inf*). They are thick and have no accessory nerve even in the larger specimens examined. They diverge obliquely posteriorly and pass through the gelatinous pillars formed by the lateral adductors of the mantle.

The stellate ganglion is typical for Octopoda. It is spherical and about 10 larger nerves originate on it; a lateral and a posterior nerve (homologous to the fin nerve of Decapoda) are the largest.

4. Visceral nerve (*n. visc*). This nerve originates on the median posterior margin of the visceral ganglion that is conically drawn out in older specimens. The visceral nerve of *Eledonella* is single for a long distance (Figures 7, 8) and divides only in the middle between brain and anus. However, in the large male of *Bolitaena* (Station 66), it was branched almost from the base, while in juvenile forms it is single for a short distance at the base (Figure 2). Each of the two branches forms a large oval ganglion at the level of the anus (Figure 4, *g. n. visc*), never before observed in any Octopod. These ganglia vary in form: in small specimens (Station 50) they are transverse-oval and situated far from the vena cava toward which they send off a thick nerve on each side. In larger specimens (Stations 49 and 53) they are oblong-oval or pear-shaped and adhere closely to the vena cava to which they also send off a short, thick branch. On these ganglia also originate two nerves for the musculature of the abdominal wall and the septum; I observed also thin branches which extend to the rectum in the specimen from Station 50. A thin branch connects the main stem of the visceral nerve with the ganglion. Because of the variability of the form of the ganglia, the nerves which originate on them are often asymmetrical. In the large specimen from Station 66, the left ganglion has two thick branches extending toward the vena cava, while the right ganglion has a single nerve which then divides into 3 branches.

As in all Decapoda, the main branch of the visceral nerve extends in a curve to the base of the gills, where it swells into a long branchial ganglion from which extends a branch to the branchial vein; the left branchial ganglion also has a branch that extends to the penis.

5. Abdominal nerve (*n. abd*). From the root of the visceral nerve there branch two nerves that have not been noticed so far. I name them "abdominal nerves" because they innervate the musculature of the inner abdominal wall, dorsal to the funnel. They accompany the visceral nerve to the exit from the cranial capsule and then curve toward the muscular lamellae. These nerves are well developed

508 already in young larvae; in *Eledonella* (Station 53) they are fused for some distance with the visceral nerve.

Nerves of the brachial ganglion

1. Brachial nerve (*n. brach*). The nerves of the arms originate on the anterior margin of the brachial ganglion (*g. brach*) and are of almost equal thickness. They are situated on the pharynx; the nerves to the 1st and 2nd arms form a curve on the dorsal surface of the pharynx. The nerves for the 3rd arms are accompanied by the brachial artery which later twice dichotomously divides and forms the large arteries of the arms. All brachial nerves are swollen at the base of the arms, forming a superficial ganglion layer which extends to the tips of the arms. Inside the arms, the nerves form thickenings that are not sharply defined and resemble a string of pearls; these thickenings alternate with the suckers. The circular commissure at the base of the arms is double and slightly zigzag-shaped.

2. Superior antorbital nerves (Figures 7, 8, *n. a. o. s*). These two nerves originate on the dorsal lateral wall of the brachial ganglion.

3. Inferior anterior ophthalmic nerve (Figure 7, *n. ophth. i. a*). This nerve originates on the ventral lateral margin, at the level of the 2nd brachial nerve.

Nerves of the supraesophageal ganglion

1. From the supraesophageal ganglion extend two pairs of commissures. One of them, the **brachio-supraesophageal commissure** (Figure 8, *c. brach. b*), extends to the arm ganglion and borders on a wide foramen between the anterior margin of the cerebral ganglion and the underlying brachial ganglion. The other commissure, the **supraesophageal infraesophageal commissure** (Figures 1, 8, *c. b. s. i*), connects the two esophageal ganglia. It is relatively long and in *Eledonella* two thick nerves extend from its proximal third to the lateral walls of the pharynx (Figure 8); I did not find these nerves in small specimens. The commissure extends to the slightly extended lateral posterior margin of the infra-esophageal ganglion.

2. Labial nerves (Figures 1, 8, *n. lab*). These two nerves extend from the dorsal side of the supraesophageal ganglion to the musculature of the dorsal skin.

Nerves of the infraesophageal ganglion

1. Infrapharyngeal nerves (Figure 5). These consist of a single median nerve which later divides, and two paired nerves the posterior of which is situated close to the buccal commissure. On first sight there appear to be additional nerves, but these are in fact the buccal artery, which extends between the buccal commissure and the sympathetic nerve, dorsal to the inferior dorsal ganglion.

2. Sympathetic nerve (Figures 1, 5, *n. symp*). Both sympathetic nerves originate on the median posterior margin of the infraesophageal ganglion, turn toward the esophagus, and extend on its ventral surface, together with the buccal artery. I never found a multiple branching of these nerves as stated by Meyer (1906, p. 253) for *Opisthoteuthis*. The sympathetic nerves end in the sympathetic ganglion (splanchnicum after Meyer, gastricum) situated to the right of the long duct which connects stomach and caecum. This ganglion is spindle-shaped and has 2 thicker and 2 thinner branches; one of the thicker nerves extends to the caecum. I did not study the exact course of these nerves.

509 ## 4. Nature and development of chromatophores*

(Plates LXXXVIII and LXXXIX)

The prevailing views on the physiology of chromatophores do not agree with the histological data. We know since BRÜCKE (1852) that there is a difference between the play of chromatophores of Cephalopoda and that of the Chamaeleontidae: electrical stimuli darken the skin of *Octopus* but lighten that of chamaeleons. BRÜCKE did not examine the fine structure of chromatophores in detail and accepted the interpretation of KÖLLIKER (1844), who discovered the fibers which radiate from the pigment spots and considered them as contractile elements responsible for the expansion of the chromatophores. Later experiments on the color play of *Sepia* are based on the excellent studies of KLEMENSIEWICZ (1879) which were confirmed by almost all authors. Like BRÜCKE, KLEMENSIEWICZ proved that the chromatophores are expanded in the active state and contracted at rest. He also showed that the nerves of the chromatophores are stimulated reflectorily from the eye and that the small ganglion pedunculi, which is situated next to the optic ganglion, is the center for this stimulation. The studies of PHISALIX (1894) suggest that a center of inhibition for the chromatophores is situated in the supraesophageal ganglion; they also prove that stimulation of all cutaneous nerves, and especially of the mantle nerve, causes expansion of the chromatophores. On the basis of these experiments, PHISALIX agrees with those who are of the opinion that the radial fibers are muscular formations and that their constant tonus causes the rhythmic expansions. If we assume with BRÜCKE that the elasticity of the membrane of the chromatophores acts antagonistically to the contractions of the radial muscles, we arrive at a physiological interpretation that agrees with the histological data. A contradictory view was published by UEXKÜLL (1892) on the basis of experiments with unipolar stimulation. He considers the radial fibers as belonging to the connective tissue and attributed the expansion of chromatophores to the action of the strongly ramified cutaneous musculature.

Physiologists thus disagree on the function of the fibers associated with the chromatophores. The controversy is even more acute among the authors who studied the microscopical structure of the chromatophores. HARLESS (1846), H. MÜLLER (1853) and BOLL (1869) confirm the existence of the fibers discovered by KÖLLIKER and consider them to be muscular, too; but HARTING (1874) rejects a closer association between these fibers and the play of chromatophores and believes that only the protoplasmic substance of the chromatophore causes its movements. Perhaps on the basis of these studies, WALDEYER (1876) states that the chromatophores are cells which make muscle-like movements "without displaying a muscular structure".

510 The nature of the radial fibers is a matter of controversy also among a number of French authors who have studied the chromatophores since 1883. Thus some of them, e.g., BLANCHARD (1883), GIROD (1883) and ALBINI (1885), believe that the fibers consist of connective tissue, while PHISALIX is convinced of their muscular nature. The view of JOUBIN (1892) that the fibers are contractile in youth but turn into connective tissue with age has not been accepted. Recent German authors, i.e., SAMASSA (1893), SOLGER (1898) and H. RABL (1900), accept the views of KÖLLIKER.

Nor is there agreement on the manner in which the chromatophores contract. BRÜCKE (1852), as already mentioned, was the first to suggest that the elasticity of the membrane may act as antagonist to the contraction of the radial muscles. Most later authors accepted this view, but held at the same time other, additional elements responsible for the contraction. BOLL (1869) described a circle of cells surrounding the chromatophore and connected it with the contraction. This "cellular envelope" plays

* Reprinted from *Verh. Deut. Zool. Ges.* (Proceedings of the German Zoological Society), 1902, p. 162ff.

an important role in later descriptions. Klemensiewicz stated that this envelope is surrounded by a fluid-filled space which he named chromatophore cavity. Phisalix also illustrated this "collerette" and stated that it becomes so dilated during expansion that it is hardly recognizable, but is distinct during contraction. In my opinion, we owe much credit to the most recent study of Rabl (1900) which disproved these ideas of an accessory circle of cells—and that, while even still Solger (1899) still clung to it and illustrated it—and described the structure of the chromatophore more simply.

There is also some uncertainty about the nature of the pigmented body of the chromatophore. A nucleus has not been demonstrated in fully developed chromatophores, and Phisalix therefore considers the pigmented area as a group of cells that have undergone degeneration of pigment. On the other hand, Phisalix and later authors, especially Rabl, stressed that juvenile chromatophores have a single nucleus and that the pigmented part has to be considered as a single cell.

The view that the activity of the chromatophore is undoubtedly controlled by the nervous system has stimulated the search for innervating fibers. Joubin (1892) proved by vital staining with methylene blue the existence of nerve fibers which originate in a cutaneous network and form a slight terminal swelling on the chromatophore without penetrating it. Samassa (1893) found a skin nerve in *Loligo* from which fibers extend directly to the pigment cell. After treatment with osmic acid, Phisalix observed a network of nerves the terminal fibers of which reach the chromatophore and branch like a tree between the pigment cell and the assumed circle of cells.

The above authors believe that the nerves end near the chromatophore or inside it, while only Solger mentions an innervation of the radial muscle fibers. Solger used vital staining with methylene
511 blue and found varicose lines or rows of granules near the insertion of muscles on the chromatophore, which he considers to be muscle nerves. Whether these indeed are nerve endings is still doubtful; later authors, e.g., Rabl, doubt it, the more so as no proximal connection with thicker nerve branches has been demonstrated.

There is thus a sharp controversy on the structure and function of the chromatophore, and not a single finding has been generally accepted. However, the recent studies of chromatophores by Phisalix and Rabl have clarified two aspects: they maintain that the radial fibers are muscular and that in young forms, the chromatophore has a nucleus. Rabl has shown that the circle of cells does not exist, while Philasix as yet maintains that it does.

All observers agree that the fibers extending to the chromatophore are cellular elements which become secondarily connected with the pigment body. Studies of the development of chromatophores have been used as evidence in support of this view.

The controversy on the structure of the fully developed chromatophore and its development is probably due to the choice of unsuitable objects. The Cephalopoda examined are all surface forms the tough, compact skin of which makes microscopic examination very difficult. The condition is different in Cephalopoda the mantle and entire body surface of which is gelatinous. Such Cephalopoda are known, but most of them are deepwater forms which are driven to the surface only occasionally, by cold deep-water currents, and have not been examined by histologists because of their rarity.

During the Deep-Sea Expedition, we repeatedly obtained such deep-sea forms, many of them in perfect condition. They include Octopoda and Decapoda the delicate, gelatinous body of which resembles that of medusae and ctenophores. This applies especially to a genus of Octopoda which appears to be the one described by Steenstrup (1858) as *Bolitaena*, the genus which Verrill (1884) described as *Eledonella*, and the one which Hoyle described as *Japetella* in the *Challenger* Report. I preserved a few juvenile specimens in formol, sublimate and Flemming's solution. Staining of a juvenile specimen with osmic acid showed all its finer structures, providing particularly valuable information.

In describing the results I begin with the development of the chromatophores, thus following the order of the examination in reverse.

Joubin derived the chromatophores from the ectoderm and showed that solid masses of cells
512 become more deeply embedded. He thinks that one basal cell of this mass becomes larger, loses the connection with the other cells and becomes the first "anlage" of the chromatophore. Mesodermal cells become arranged radially around the basal cell and later grow into the radial fibers.

As stated above (p. 387), this concerns the development of the tufts of bristles and not of chromatophores.

Contrary to Joubin, later workers consider the chromatophores as mesodermal formations. Girod and Phisalix reported on mesodermal cells the protoplasmic processes of which anastomose and form a more or less dense network. Some of these cells, distinguished by their large size and different structure of the nucleus, develop later into young chromatophores. We noted above that Phisalix thinks that the pigmented chromatophore grows at the expense of peripheral cells. Like all the other observers, Girod and Phisalix accepts the view that cells surrounding the chromatophore form the radial fibers. Rabl, too, derives the chromatophore from cells of the cutis; he finds, however, that the young chromatophore is surrounded by a sharply differentiated membrane to which extend the later muscles, some of which are broom-like branched. It would lead us too far off to enlarge on these data or on the occasional observations on the development of chromatophores reported by other authors, the more so as none of them observed the earliest stages of development of the chromatophores.

Turning now to my results with *Bolitaena*, I would point out that sublimate and osmium preparations give good results, with slight differences due to the method of preservation.

It seems advisable to describe first the structure of the outer skin of these gelatinous forms. The ectoderm consists of markedly flattened, elongate cells, many of which contain numerous granules. The epithelium is usually chafed off, a condition that facilitates the study of the deeper parts. The cutis is gelatinous and contains very fine fibrils. The cellular elements consist of numerous rounded or oval connective tissue cells. Also present are capillaries and, in particular, a well-developed network of nerves (Plate LXXXIX, Figure 1, *n*). This network is very distinct and can be followed clearly from the thicker stems to the terminal branches, as in transparent Heteropoda. The thicker nerves originate on the mantle ganglion. They are usually accompanied by blood vessels and gradually divide into thinner branches which finally form the terminal network. At the point where the thinner nerves branch, there is a usually plate-shaped widening which is usually triangular and in which the nuclei are situated; these are usually oval and finely granulate, but sometimes homogeneous and strongly refractile. The functional chromatophores of some specimens are arranged in regular longitudinal and transverse rows (Figure 9). This arrangement corresponds to the characteristic formation of the
513 upper muscular layer which consists of longitudinal and transverse cords that extend almost perpendicularly to each other. The larger chromatophores usually follow the direction of the muscle cords and are often situated at the corners of the square fields of muscles. It is in connection with the transparency of the gelatinous mantle that the chromatophores pass also to the inner side of the mantle margin and even to the visceral sac (Plate LXXXIV, Figure 1).

The development of the chromatophores is connected with cells of connective tissue of the gelatinous cutis. These cells are usually scattered, rarely forming nests, and are never branched. They are 0.02 mm large and are usually oval, rarely spherical (Plate LXXXVIII, Figures 1, 2, 3). The large spherical nucleus is eccentric at one end of the ovoid cell. The nucleolus is usually central, rarely peripheral, and is surrounded by a shell-like arrangement of chromatin bodies. The dark, finely granulate

plasma contrasts sharply with the light-colored nucleus. The nucleus constantly borders on a darker sphere which iron hematoxylin staining reveals to have a small central granule. In a few cases I found fine fibrils which extend from the central granule to the peripheral granules of the sphere (Figures 2–7).

These cells are usually isolated in the gelatinous tissue, so that the remarkable transformations during development of these cells into young chromatophores are clearly recognizable. The cells become at first slightly larger and show a separation of their content into a light-colored ectoplasm and an endoplasm which contains the nucleus and the dark sphere. From the ectoplasm extend short, pseudopoda-like processes (Figures 4–6). They are usually few in number, but even if more numerous, those that will attain dominance, become rapidly longer and occasionally anastomose with adjacent strings will only be few. The number of radial processes varies from 9 to 14; rarely are there more or fewer. All the larger processes are situated in a plane parallel to the surface of the body.

When the early "anlage" has assumed a stellate form, a secretion of contractile substance is distinctly visible in the processes (Figures 8 and 9). Cross sections of the processes show that the contractile layer forms two separated lateral zones along each fiber which stain light-greenish in osmium preparations. Between these zones extends a light-colored, sometimes slightly undulate slit along the whole process. For reasons which will be discussed later, it is important that the contractile substance is secreted not only along the processes but also in a ring which connects their bases. There are thus two systems of contractile bands: one is radial, the other forms a ring adhering to the cell membrane.

The cell is transparent at these stages because of the abundant cell fluid, and only little granulate protoplasm is present around the nucleus. The latter begins to divide, but karyokinetic figures are
514 definitely absent throughout these divisions; often, however, the nuclei assume the form of a dumbbell: an indication of direct division. Stages with 2–5 nuclei are common. The newly formed nuclei are rounded, oval or almost triangular and always homogeneous and highly refractile. The nuclei stain intensively with different stains. I sometimes found that one nucleus differs from the others in being weakly refractile and finely granulate. However, I was unable to derive any rule for this irregularity; sometimes the first two nuclei were identical, sometimes they differed as described above. In stages with 3 and 5 nuclei, I most frequently found a finely granulate nucleus near two homogeneous nuclei. Most common were stages with 8 completely homogeneous nuclei of almost the same size, measuring 0.008 mm (Figures 8–12).

During this multiplication of the nuclei, the cell is about 0.035 mm wide and shows further transformations. The part of the cell closer to the surface begins to protrude and contains numerous, strongly refractile flakes of irregular form. They stain much less intensively than those nuclei that are now situated in the lower, sometimes irregularly sinuate half of the cell. In stages with 8 nuclei the cell is longest, because the upper part of the cell containing the flakes becomes extended like a cone (Figure 10). The boundary between the two halves of the cell is marked by the ring of radial fibers and the ring-shaped contractile zone.

The radial fibers have grown to twice or 3 times the width of the cell. Considering the large number of nerves in the gelatinous skin, it is not surprising that the ends of some radial fibers come into contact with thin nerves, forming nerve endings which could be demonstrated with all desirable clarity in all the young chromatophores examined.

The nerve endings (Figures 8, 9, 11, 12) are of varying form. The end of a radial fiber frequently reaches a nerve and passes broadly into it. The end plate formed is usually triangular and there is no distinct boundary between nerve and fiber. The end plate often contains a large, finely granulate

nucleus (Figure 8). Sometimes two and even 3 radial fibers become fused with the nerve, each time forming a slight widening at the point of fusion. If the young chromatophore is situated near the branching of a nerve, most of its radial fibers may become innervated. On the other hand, the fiber often does not end at the nerve but continues with its contractile substance beyond the nerve, so that a nearly square connection between fiber and nerve is formed. It is not certain whether the innervation is caused by accidental contact with the growing radial fibers or whether the nerves search for the young
515 chromatophore. What is certain is, first, that the innervation concerns exclusively the radial fibers, never the body of the cell, and second, that not a single chromatophore was found in which not at least one process was in contact with a nerve.

The cell undergoes important changes in stages with 12–16 nuclei. The chromatophore becomes flattened and wider. The refractile flakes in the upper half of the cell lose their sharp outline and gradually disappear. Seen from above, the cell membrane shows fine wrinkles in the form of undulate lines (Figure 13). One of the 12–16 nuclei was often slightly larger than the others.

It soon becomes clear that this is a young chromatophore. The flakes are replaced by a coarsely granulate, slightly yellowish or reddish pigment which fills the upper surface of the strongly flattened "anlage". The nuclei formed by the last division move rapidly away from each other and form a ring at the periphery of the cell. Only the larger nucleus mentioned above remains in the center of the chromatophore. It contains 1–3 large, strongly refractile nucleoli, while the nucleoli of the finely granulate peripheral nuclei can hardly be distinguished from the other granules. The difference between the homogeneous, usually spherical central nucleus with its very large (0.008 mm) nucleoli and the peripheral, smaller, usually oval and finely granulate nuclei becomes increasingly distinct. The number of peripheral nuclei is variable. There are usually 28 ones (Plate LXXXIX, Figures 5 and 6). Stages with 32 peripheral nuclei were also present; others had as few as 18 nuclei.

The polynuclear cell becomes markedly flattened and the fine wrinkles of the membrane disappear. The pigment becomes finely granulate and fills that half of the cell that faces the surface. It expands toward the peripheral nuclei; the margin of the originally cap-shaped upper part may still show a sharp outline. When, however, the upper half of the cell has become completely flattened, this sharp margin either disappears or remains visible in only one half of the cell. The lower half of the cell also becomes flattened but contains no pigment and shows a honeycomb pattern of protoplasmatic substance in the homogeneous cell fluid. The nuclei at the disc-shaped margin of the cell gradually move into onion-shaped swellings of the lower half of the cell.

These stages look particularly decorative, due to the continuation of the onion-shaped swellings with nuclei into contractile radial fibers that are connected by numerous anastomoses. The chromatophore now resembles a rhizopod with thicker and thinner pseudopodia. The network of radial fibers
516 is shown in Figures 5 and 6, which are drawn from osmium and sublimate preparations.

The above stages have been described by earlier authors. Some of the drawings, e.g., those of Phisalix and Rabl, show a likeness to the condition described here, although they were quite differently interpreted.

The development to a functioning chromatophore proceeds as follows. The whole "anlage" becomes wider, the pigment reaches the peripheral nuclei and sometimes continues in the form of a cord into the radial fibers. The sharp contrast between the upper and lower half of the cell disappears, and the large central nucleus is now surrounded by pigment inside a dome which slightly protrudes. This nucleus, which is 0.025 mm in size, could be demonstrated in all expanded old chromatophores.

The radial fibers draw out like a spider's web, to considerable length, while the lateral anastomoses disappear. Remnants of anastomoses persist rarely at the basal widening of the fibers. The contractile

substance becomes divided into thin bands which are recognizable for some distance beyond the nucleus. Contrary to the data of Girod and others, the radial fibers are not branched. They end rarely free and are usually connected with the underlying network of the superficial muscular layer. A direct connection between the fibers of adjacent chromatophores, which was reported by some authors, has not been observed, but two fibers of adjacent chromatophores may be situated on the same mesh of the underlying musculature (Figure 1, left). If the chromatophore expands, the radial fibers become contracted to half and even a third of their normal length and swell near the base.

The nerve endings at the fibers of fully developed chromatophores are not as clearly recognizable as in the younger stages. It is only rarely possible to demonstrate a connection between a nerve and an underlying fiber. The number of radial fibers equals that of the peripheral nuclei, but two nuclei may sometimes enter the same onion-shaped swelling and apparently become fused later. The chromatophores that develop during the embryonic stage apparently have fewer radial fibers than those which which develop later. The oldest chromatophores have only 16–20, those which develop later, 28–32 radial fibers.

The above-described observations should be seen to show the structure as well as the function of the chromatophore in a new light.

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517 The most important conclusion from the above concerns the morphological value of the chromatophore; I arrived at this conclusion by way of its developmental history. This conclusion, however, contradicts all other observers. The embryological development proves that the chromatophore is not formed by a secondary union of originally separate cellular elements but is a single complicated cell with numerous nuclei. Only one larger nucleus of deviate form remains in the center of the chromatophore, the other nuclei move to the periphery and develop into centers for the contractile processes. The resemblance to Protozoa is distinct. Some Metazoa have cells which have multiple functions and this is expressed in their form, for example, the cnidoblasts of the Coelenterata; were this not known, we would be surprised that even in the more developed Cephalopoda we find radial muscular fibers with a central pigment body occurring within a single cell that is characterized by the different structure of its nuclei.

We have proved that the connection of the radial fibers with the pigmented part is not secondary but that the fibers radiate originally from this part, like pseudopodia. Some earlier data can therefore be interpreted differently. It was only with reserve that careful observers have been mentioning a boundary between the pigment body and the basal part with fibers. Some authors admit that a separating membrane is not recognizable. The penetration of strands of pigment beyond the nucleus and into the radial fibers could hardly be explained if a membrane were present between the chromatophore and the radial fibers. If Rabl is convinced that the young chromatophore and the radial fibers are separated by a membrane, this is due to the fact that the pigmented upper part of the cell has not yet become flattened at the margin but is separated from the lower half of the cell by a ring-shaped fold which may be mistaken for a limiting membrane.

Embryology also explains some points concerning the function of chromatophores. It proves Kölliker's view that the fibers are contractile and cause the chromatophore to expand. This view has been repeatedly, and correctly, maintained and I refer only to the description of the nerve endings at the radial fibers. These nerve endings could not be explained unless the radial fibers are considered as contractile elements. Contrary to Uexküll's assumption, participation of the body musculature in the expansion of the fibers must be excluded in view of the position of the muscular layers under the chroma-

tophore. Furthermore, Phisalix, and later Steinach (1900), proved that Uexküll's views are untenable. They have shown that the chromatophores move while the musculature of the body remains inactive, and that the peristaltic movements of the musculature do not conform with the chracteristic "pulsations" of chromatophores.

Since Brücke, the elasticity of the strongly expanded cell membrane has been held responsible
518 for the contraction of the chromatophore. According to my observations, this membrane may, indeed, take part in the contraction but is not alone responsible for it. The contractile substance is secreted not only in the radial fibers but also at the margin of the cell. This substance does not disappear in later stages but extends in a curve between the base of adjacent radial fibers, as can be shown in expanded chromatophores. The contraction of this substance obviously acts antagonistically to the traction of the radial fibers. As the muscular bands are in a constant tonus, it depends, in my opinion, on whether the radial or the curved tractional direction predominates. The chromatophore contracts if the curved traction predominates; it expands if the resistance of the curved traction is overcome by the radial fibers. The characteristic concavity of the margin of the expanded chromatophore between two radial fibers is caused mainly by the contraction of the curved fibers.

5. Eye

The eyes of Bolitaenidae (Plates LXXXI–LXXXIII) are generally moderately large and more or less oval. Sometimes they are slightly ovoid, since the dorsal part of the eyeball is slightly wider than the ventral part. In distinctly oval eyeballs, the longitudinal axis of the eye is situated obliquely to the transverse axis of the body. The eye of the largest specimen of *Bolitaena* was 12 mm long and 8.5 mm wide; the lens was 4.3 mm wide. The eye of *Eledonella* was 10 mm long and 8.5 mm wide, and the lens was 4 mm wide. In a male *Eledonella* with a hectocotylized 3rd arm the eyes were 5 mm long and 4 mm wide. The eyes of *Bolitaena* usually are more distinctly elliptical than those of *Eledonella*, the ratio between length and width being 6 : 4 and 5 : 4. Some juvenile forms have more distinctly elliptical eyes.

The eyeball is usually blackish brown; in *Bolitaena* it has a metallic sheen on the outer side and on the iris (Plates LXXXII and LXXXIII); in *Eledonella* (Plate LXXXI) the pigment is less marked and the iris is brown in life.

One detail is apparently unique among the Octopoda, i.e., the formation of lid folds on the anterior side of the eye. It is characteristic for the Octopoda that the lid fold covers the lens and pupil and develops into a cornea; moreover, there are often secondary duplications which, too, have been described as eyelids. The Bolitaenidae do not show these complicated structures on the anterior surface of the
519 eye; rather they resemble the Oegopsida so closely in this respect that this very fact proves that the systematic value of eyelids in the classification of Cephalopods should not be overestimated. As already noted in the description of the eye of *Spirula*, the form of the lid fold does not prove that this genus belongs to the Oegopsida. The conditions are similar in the Bolitaenidae.

The lid fold of *Eledonella* is exactly as in the Oegopsida. The lens is entirely free in all preserved specimens, and the opening of the lid fold is as wide as that of the lens. It is therefore not surprising that the eye occasionally protrudes while the margin of the lid folds recedes. In *Bolitaena* the opening of the lid fold at maximal contraction was slightly narrower than in *Eledonella*. In the large specimen from Station 66, the opening on both eyes was situated behind and dorsal to the opening of the pupil.

The pupil may form a slit or be horseshoe-shaped, depending on the contraction of the iris.

Observation of the live animal shows that the horse-shoe form is due to the fact that the posterior margin of the iris projects in the form of a kidney-shaped lobe.

Although sections of the eyes of two small specimens of *Eledonella* showed no important differences from the condition in other deep-water Cephalopoda, they are of sufficient interest to merit a brief description.

The eye of a young *Eledonella* from Station 44 is 3.7 mm long. The delicate eyeball is stiffened by a cartilaginous lamella which extends from the ciliary body to the margin of the white body. Circular muscle fibers on the eyeball are only moderately developed. The eyeball is enveloped by dense chromatophores. The optic ganglion is not situated exactly in the main axis of the eyeball but slightly posteriorly. It is kidney-shaped, with a deep dorsal groove. Its layers correspond to those in other Octopoda. The white body is ring-shaped and thickened on one side in its posterior half.

The layer of nerve fibers which extends into the granulate layer of the retina is normal. The sensory cells are densely arranged, with oval nuclei which have numerous chromatin granules. The abundance of sensory cells is demonstrated by the fact that they are arranged in 5–6 stacked layers of nuclei. The cells of the limitans are sharply differentiated from the visual cells; their nuclei are arranged in a row at the base and are narrower than the nuclei of the retina from which they also differ by their intensive staining. The pigment is in the typical dark position, forming a thick layer at the base of the rods. The figure shows that the dark adaptation observed here does not differ from that in the retina of other deep-sea Cephalopoda. The rods, although not very long, are as long as the retina is thick.

520 The anterior margin of the retina does not reach the base of the ciliary body; the rods here become very thick. The pigment of the retina extends on the inner side of the not very large ciliary body; the inner epithelial lamella of the ciliary body is slightly pigmented, while the outer lamella, which secretes the outer half of the lens, is not pigmented.

The iris is also pigmented on the inner side, especially at the margin of the pupil. It contains numerous lamellae of connective tissue which form a reflecting layer and cause the metallic sheen. These lamellae stain deep-black with iron hematoxylin. The reflecting layer of the iris extends on the eyeball almost to the level of the margin of the retina. The lid fold contains numerous well-developed circular fibers which cause the constriction of the opening.

6. Static organs

(Plate LXXXVI, Figures 1–8)

The static organs are situated on the ventral side of the brain and are 2–3 times as large as the brain. Each static organ (Figure 6) is enveloped by an ovoid capsule (*caps*) the longitudinal axis of which is directed obliquely to that of the organ. The capsules are contiguous, and thus flattened, in the midline. Directly in front of them are situated the two uniting arms of the vena cava (*c. v. br*), near which the anterior and posterior funnel nerves (*n. inf. a* and *n. inf. p*) are visible. The visceral (*n. visc*) and abdominal (*n. abd*) nerves are visible at the posterior margin of the capsules. The capsules are filled with a fluid that may be named perilymph, and the static organs are situated inside them; the latter are only about half as large as capsules and contain endolymph.

These shining, thin-walled but resistant capsules are the last remnants of the cranial cartilage; this is proved by the remnants of cartilage that are still present in the middle on the dorsal side of the capsule and surround the funnel nerves and the adjacent vein. Sections of this area show that the structure of the cartilage resembles that of the fin cartilage of *Chiroteuthis*. The hyaline substance has

a reticulate structure and at some points the meshes are so small that they look like thin membranes of the large cartilage cells. The hyaline substance becomes more prominent near the wall of the capsule, while the cartilage cells become smaller. The wall of the capsule has a homogeneous structure, with large cells embedded. It stains exactly like the cartilaginous substance.

The statocysts (Figures 1, 5, 6) are oval, thin-walled and sometimes situated so closely together that they are almost contiguous in the middle. The space of the capsule, which is filled with perilymph, contains only sparse vessels and tissue of the wall of the capsule (Figure 8). The arterial vessels branch
521 from the orbital artery. They become ramified near the wall of the statocyst and form a delicate but not dense capillary network. The conical processes, characteristic for the statocysts of Decapoda, are absent in the Octopoda. As JOUBIN has shown, only *Cirroteuthis* has a few such processes. The statoliths are silvery structures situated on an oval pad (Figures 1, 2). Seen from above the statoliths are also oval; they have a knob-shaped thickening at the end opposite the nerve; in lateral view they are seen to constitute a plate that is thickened on one side and surrounded by a groove. In addition to the sensory pads—named by HAMLYN-HARRIS (1903) "macula statica princeps" (Figures 1, 2, 3, 5, *mac. st*)—there is a crista (*cr*) which consists of sensory epithelium, too. It begins near the macula princeps on the dorsal side of the statocysts, then turns to the ventral side in a spiral, and finally again ascends to the dorsal side (Figures 1, 5, 6, *cr*, *cr. stat*). Contrary to the accepted view, the static nerve (Figures 1, 5, *n. stat*) is divided into 3, not 2 branches. The shortest branch (*n. stat.*^{1}) extends to the narrow proximal side of the macula princeps, the two other branches (*n. stat*^{2}, *n. stat*^{3}) innervate the crista. The anterior branch (*n. stat*^{3}) reaches the crista at its beginning, some distance from the macula princeps; the posterior branch (*n. stat*^{2}) reaches the crista only near the end. Microscopic examination shows that both branches divide like a fan into fine fibers (Figure 7) which form a wide band of exceedingly fine fibers on the homogeneous outer side of the crista. The long nuclei of the nerves, which are sometimes arranged in a row (Figure 4, *n. st*^{3}), are recognizable only with difficulty.

I made sections of the sensory pad. The object is, however, not very suitable for microscopic examination; still, the large sensory cells with their fine hairs, and the small elements which HARRIS names "supporting cells", could be identified. The sections also showed that the delicate wall of the statocyst thickens beneath the macula princeps and the crista into a cartilage-like tissue in which the embedded cells are distinctly visible.

7. Vascular system

(Text Figures 62 and 63)

Satisfactory information on the structure of the vascular system cannot be expected from the preparation of two relatively small specimens. Only injection can give information on such minute details as, for instance, the dilatations of the veins around the pharynx and near the stomach. The following description therefore contains only data which could be determined and illustrated with certainty.

Arterial circulation. The heart of *Bolitaena* and *Eledonella* is almost pear-shaped. It is situated
522 dorsal to the right branchial heart, between the right renal sac and the testis. Its longitudinal axis extends obliquely from its anterior end on the left side to the right and posteriorly; it also descends slightly to the ventral side and anteriorly. The heart is wider anteriorly, where it extends into the cephalic artery (Text Figure 62, *a. ceph.*). Its anterior margin is surrounded by the closely approximated branchial veins (atria) the valves of which are clearly visible on the transparent heart. Between the atria

originates a thick artery which was named by NAEF "anal artery" (*a. anal.*). It is directed dorsally and divides into several branches. The anal artery has two branches near the heart, one of which extends ventrally to the gelatinous substance of the septum and may therefore be named "septal artery" (*a. sept.*). The other branch is the artery of the vas deferens (*a. v. def.*, *a. ves. sem.*); it passes anteriorly and in close prixmity to the left branchial vein, then crosses it in a curve, reaches the inner surface of the envelope of the gonoducts, and divides there into two branches, one of them directed anteriorly and the main branch directed posteriorly to the ampulla.

MEYER (1906, p. 211) described in *Opisthoteuthis* a genital artery which apparently corresponds to the above-mentioned branches of the anal artery since it also supplies the seminal vesicle. The proper genital artery ("testicular artery" in his terminology) was, however, considered by him as a branch of the anal artery. This is not the case in the Bolitaenidae. The genital artery (*a. gen.*) of this family originates on the posterior margin of the heart as an independent vessel which reaches the anterior

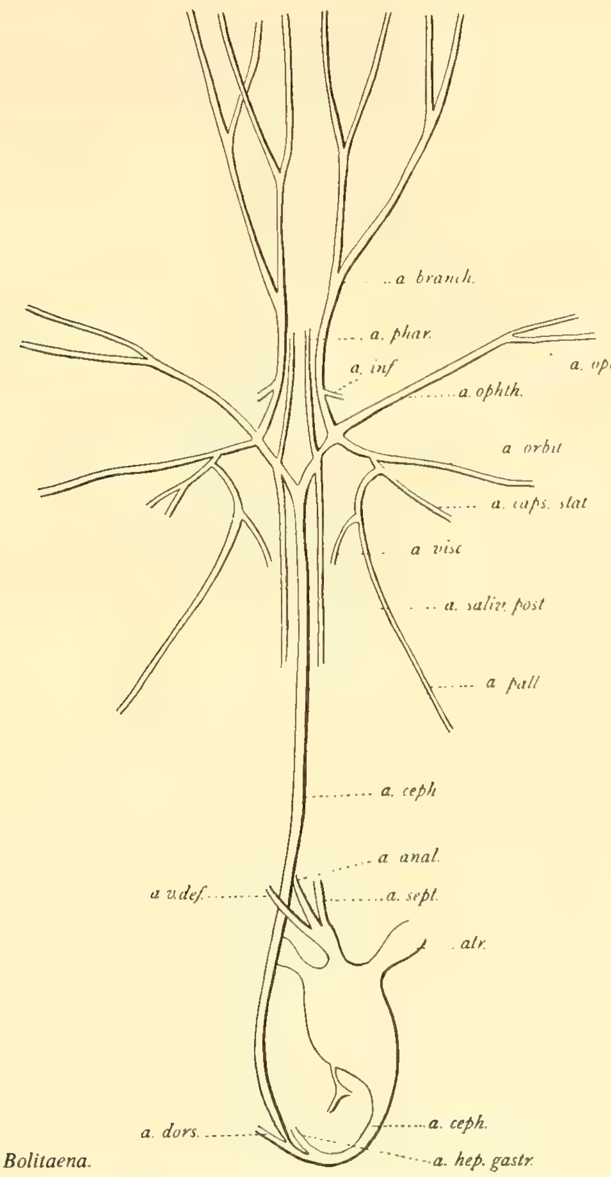

FIGURE 62. Arterial circulation of *Bolitaena*.

margin of the testis and enters it. This independent origin of the genital artery was established in the 3 specimens which I examined.

A third vessel originating separately from the heart is the cephalic aorta (*a. ceph.*), which begins on its apex. The cephalic aorta of the large male extends obliquely posteriorly and dorsally on the right anterior side of the testis, then curves around the right posterior outer margin of the liver, descends between the right salivary gland and the esophagus and then extends on the right side of the esophagus.

523 The hepato-gastric artery (*a. hep. gastr.*) branches proximal to the aorta. It descends deeply at the level of the apex of the liver, passes on the right side between stomach and caecum above the posterior end of the gastric ganglion, and then enters into the liver and has a branch to the pancreas.

Near the hepatic artery extends a thin vessel which branches from the aorta and is directed dorsally. It probably corresponds to the dorsal artery (*a. dors.*).

The other vessels that branch from the aorta and extend along the esophagus have not been followed, but one of them branches on the crop.

As in all Cephalopoda, the aorta of *Bolitaena*, extending on the dorsal side of the esophagus, divides into two main branches. Two thin vessels, the salivary arteries (*a. sal. post.*), branch from the middle of the aorta and extend to the posterior salivary glands. At the same level originate two thick branches which extend anteriorly, pass through the esophageal commissure together with the esophagus and extend to the pharynx, where they surround the buccal ganglion. These are the pharyngeal arteries (*a. phar.*).

Further on from the point where the above-mentioned vessels branch off, the two main arms of the aorta form a number of branches on each side. The median stems continue for a short distance along the esophagus and then enter the ventral mass of the brain at the border between the pedal ganglion and the visceral ganglion.

Near their entrance into the brain, the main branches have two thin branches: the cerebral arteries. After their exit from the ventral mass of the brain they have a thin branch (*a. inf.*) which accompanies the anterior funnel nerves (*n. infundibuli ant.*). The two branches then pass on the ventral side of the pharynx and twice divide dichotomously to form the 4 brachial arteries (*a. brach.*) for the arms. The bifurcation for the 1st and 2nd arteries is situated slightly posterior to that of the 3rd and 4th arteries.

The median of the 3 vessels that branch from the branches of the aorta is the ophthalmic artery (*a. ophth.*). It extends obliquely anteriorly outward toward the optic nerve, to which it sends off the arteria nervi optici (*a. opt.*); the main stem of the ophthalmic artery extends above the optic ganglion and branches at the base of the eyeball.

The outer branch may be named orbital artery (*a. orbit.*). It accompanies the inferior ophthalmic nerve from the beginning and ends on the posterior side of the eyeball.

One of the branches at the base of the orbital artery is the thick pallial artery (*a. pall.*), which accompanies the pallial nerve. At the base of the pallial artery begin thinner vessels (*a. cap. stat.*) which branch on the static capsule. The pallial artery has also a thin branch (*a. visc.*) to the visceral nerve and accompanies it for a long distance.

524 **Venous circulation** (Text Figure 63). Two thick stems extend in each arm; they unite at the base and open into a venous semicircle (*arc. ven. brach.*). They form the two arms of the vena cava (*v. c.*), which receive at their confluence the ophthalmic veins (*v. ophth.*) on each side. Each ophthalmic vein originates in a large venous sinus which surrounds the optic ganglion. At the opening of the ophthalmic veins into the vena cava are situated two valves which also prevent the return of blood from the lower vena cava. Ventrally the vena cava receives the funnel vein (*v. inf.*), which is formed by the union of two main branches. The two orbital veins extend superficially on the posterior margin of the eye,

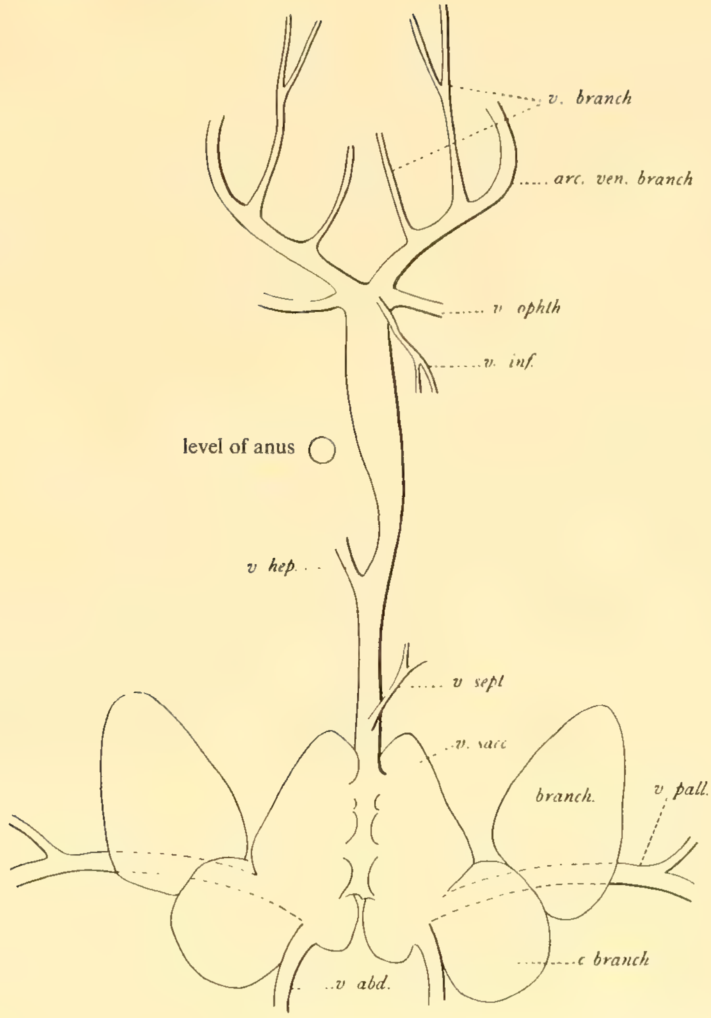

FIGURE 63. Venous circulation of *Bolitaena.*

near the margin of the collaris. This union of the two arms of the vena cava is of topographical interest, and it should be mentioned that both posterior infundibular nerves extend anteriorly between the two arms, while the anterior infundibular nerves are situated behind the confluence. The adductor nerves are visible laterally.

The unpaired vena cava is situated ventrally to the static organs. In front of the anus it bends slightly to the left and then extends straight without any dilatation or branching until it opens into the venous sacs (*v. sacc.*). The vena cava receives the hepatic vein (*v. hep.*) half way along the intestine; this vein becomes ventrally visible on the middle of the liver and extends obliquely to the left toward the vena cava. Since it seems that the hepatic vein has so far never been described in detail, I may add that its above-described condition was distinctly determinable in a younger specimen.

Before the vena cava enters the area of the renal sacs, it receives the vein of the septum (*v. sept.*), which is the counterpart of the artery of the septum.

The vena cava extends straight between the two renal sacs toward which it gradually divides into branches to the two venous sacs. The latter are bean-shaped, smooth on the ventral side, and 8 mm long in the specimen examined (Station 66). They widen posteriorly and dorsally and their dorsal
525 part forms a rounded swelling. There is a curved groove near their lateral posterior margin which is occupied by the openings of large collecting veins, mainly the abdominal vein; the spongy tissue

of the groove is visible. The pallial vein (*v. pall.*) opens into the venous sac somewhat anterior to the opening of the abdominal vein. The pallial vein receives the venous blood from the branchial gland; it also receives the vein from the stellate ganglia.

The branchial hearts (*c. branch.*) are situated close to the posterior outer wall of the venous sacs so that only a short, wide opening on the median anterior wall of the branchial hearts connects them with the venous sacs. The branchial hearts are situated close together; they are 5 mm wide in the specimen from Station 66. The vas afferens (branchial artery) extends from the anterior outer wall of the branchial heart to the gills. The two valves at the base of the vas afferens are distinctly visible in young specimen, even without preparation.

8. Gills

(Plates LXXXIII and LXXXIV)

The gills of the specimen from Station 66 are 11 mm long and 7 mm wide posteriorly. The gills are short and thick, with 7 outer lamellae the anterior one of which is very small; the posterior lamellae, especially the 2nd and 3rd, are the longest. The 6 inner branchial lamellae are only about half as long as the outer ones, so that the outer lamellae are free toward the branchial gland and the canal of the gills is exposed. The branchial gland is 8 mm wide and does not reach the base of the gills. The vas afferens passes near the posterior end of the branchial gland. The gills of juvenile specimens are brownish.

The branchial vein (vas efferens) extends from the median crest of the gill, continues to the left on the inner margin of the renal papilla and turns obliquely toward the heart. As the heart is situated behind the right renal sac, the left vas efferens is longer than the right one. Both open anteriorly and laterally into the truncate anterior wall of the heart.

9. Intestinal tract

(Plate LXXXVII)

The intestinal tract of the Bolitaenidae shows a number of characters which, though being of some importance for the determination of the family, are readily in agreement with the group. A layer of large chromatophores covers the whole intestinal tract except the rectum; their coloration is so vivid that it shows the position of the pharynx and the middle parts in the half-transparent body already from the outside.

Pharynx (Figure 1, *ph*). I made longitudinal sections of the pharynx of a medium-sized specimen of *Bolitaena* from Station 50. The pharynx is 8 mm long. It does not show the gelatinous consistency
526 which is characteristic for the family. This and the relatively large size of the jaws suggest a strong musculature: the masticatory muscles, which move the radula, are well developed, and so are the muscles of the jaws (the so-called swellings of the jaws) the form of which reproduces exactly that of the jaws. The pocket of the tongue, which consists of two lamellae that surround the tongue laterally and are connected posteriorly and ventrally with the common muscular mass at the base of the pharynx, resembles the condition in *Polypus*.

The pharynx contains a ventral muscular cone which is named subradular organ (Joubin calls it "tongue"). It is separated by a deep fold from the tongue proper. That half of the organ that faces

the tongue bears the only gelatinous part in the area of the pharynx. That part of the subradular organ that faces the submaxillary gland projects into a papilla on which the efferent duct of the posterior salivary gland opens.

HEINRICH (1904) describes as "tongue" the entire muscular swelling on which the radula is situated. It has no cartilaginous radula supports, and the entire part consists only of a strongly developed mass of supporting and motor muscles, namely the protractors and retractors of the radula.

The pocket of the radula is very large and wide; it curves ventrally and its dilated posterior part projects beyond the infrabuccal ganglion. The submaxillary gland is large and well developed; it was named "glande sousmandibulaire" by LIVON (1881) in the Octopoda, and "glande sublinguale" by JOUBIN (1887) in *Sepia*; WÜLKER (1909) described it in several Decapoda. Some observers describe it as a complex of glandular sacs situated on the subradular organ and this is also the case in *Bolitaena*. However, the submaxillary gland is not restricted to this area but represents an elongate sac the ventral epithelium of which consists of a single layer which forms a smooth or slightly sinuate lamella, while the dorsal surface, which is situated on the subradular organ, shows the follicles mentioned above. The glanular epithelium is of varying structure. Dorsally, at the opening of the sac, there is a follicle which is lined with light-colored cylindrical cells. The same cells are present also on the smooth ventral side, while the mass of the follicles consists of intensively staining epithelial cells which are not very high.

A ganglion is situated in the muscular mass of the subradular organ. It was described by PELSENEER (1899, p. 56, Plate XXII, Figures 184, 185) as "ganglion subradulare" in embryos of *Sepia*. Two long commissures connect it with the infraesophageal ganglion. In *Bolitaena* this ganglion is situated in the middle of the gland and is relatively small.

527 The **esophagus** (Figures 1–3, *oes*), which begins on the dorsal side of the pharynx, is relatively slender and embedded in a blood sinus which I named "cephalic vein" in the Oegopsida. It contains also the salivary duct and the cephalic aorta; the latter bends at first to the right and then to the dorsal side between the posterior salivary glands. At the level of the union of the two salivary ducts, the esophagus leaves the blood sinus, widens posteriorly and opens into the large crop (*ingl*) which is widened toward the liver and has relatively thin walls; in one specimen it was filled with food. The esophagus widens behind the crop into a short duct which opens into the stomach (*st*). A cross section of the the esophagus of a young specimen showed about 7 folds which project on the outside; the lumen of the esophagus was lined with a relatively thick cuticle.

The **stomach** (*st*) and **caecum** (*st. coec*), also called "muscular stomach" and "spiral stomach", are relatively small compared with the liver; they are separated by a wide duct.

The **stomach** (Figures 1–3, *st*) is situated obliquely to the median plane and is 11.5 mm long in the large specimen from Station 66. It is acorn-shaped and has a well-differentiated terminal dome. Its strong musculature consists of 3 layers, a sickle-shaped muscular pad (Figure 3, *a*) which extends from the opening of the esophagus and covers the anterior part slightly asymmetrically, and two large lateral pads (Figure 3, *c*) which are separated dorsally and ventrally by thin, slightly convex layers that are covered with shining connective tissue (Figure 3, *b*). The musculature of the acorn-shaped terminal dome is more weakly developed than that of the pads (Figure 3, *d*). These layers are sharply defined in the empty stomach. When the stomach is filled the boundaries disappear and the acorn-shaped terminal dome becomes dilated.

Transverse and longitudinal sections through the stomach of a young specimen show that the lumen is compressed by the lateral pads. This middle part of the stomach contains a folded layer of epithelium with a very thick intima. Connective tissue enters between the folds. Longitudinal sections

also show that the terminal part is sharply differentiated from the muscular pads and that its lumen contains more numerous folds than the middle part, but its cuticle is thinner. This suggests that the terminal part is very extensible.

The **caecum** (Figures 1, 2, *st. coec*) is connected with the stomach by a moderately wide transverse duct to which the gastric ganglion (*g. gastr*) adheres on the right side. The caecum lies slightly more anteriorly than the stomach and adheres to the posterior side of the liver beyond which it projects in lateral view. It is rounded in ventral view (Figure 2), 68 mm wide [*sic*; =6.8 mm], and shows a heart-
528 shaped indentation anteriorly in which the hepato-pancreatic duct (*d. hep. pancr*) is situated. Numerous radial folds extend from this indentation.

The **intestine** extends dorsally from the dorsal wall of the caecum, i.e., from the side which borders on the liver, between the hepato-pancreatic ducts and in the direction of the connecting duct (Figure 2). It is wide, with straight folds and extends anteriorly, covers the relatively small ink sac (*atr*) in the middle, then becomes narrow and continues gradually into the rectum (Figures 1, 2, *rect*).

The anus (*an*) projects beyond the apex of the liver (*hep*) and has simple lobes with narrow, pointed anal appendages.

Salivary glands (Figures 1, 3). The anterior salivary glands (*gl. sal. a*) are situated dorsally on the pharynx, lateral to the base of the esophagus; their posterior margin borders on the infraesophageal ganglion.

The posterior salivary glands (*gl. sal. p*) are relatively small in young specimens but apparently become very large with age. They are 17 mm long in the specimen from Station 66, i.e., six-sevenths of the length of the liver. This gland's large size may be connected with its function as poison gland. The glands are oblong-oval and their efferent ducts begin in the middle of the median margin. The ducts soon unite into a single duct (*d. sal*) which passes into the venous sinus on the right and slightly ventral to the esophagus. Next it passes through the brain, and then to the ventral side of the pharynx, enters the muscular mass behind the submaxillary gland, continues directly over it, and opens on a papilla of the subradular organ.

The **liver** (*hep*) is longitudinally oval; it surrounds the caecum posteriorly, borders posteriorly and laterally on the stomach, and with its truncate dorsal surface on the crop and salivary glands. Anteriorly the liver extends almost to the level of the anus. Its surface shows a honeycomb structure which is caused by the polyhedral hepatic follicles. The liver has a silvery capsule. As in all Octopoda, the liver of the Bolitaenidae is large; in the specimen from Station 66 it is 21 mm long and 11 mm wide.

The ventral posterior side of the liver bears two yellowish packets of glands which are 5–6 mm wide and contrast sharply with the dark-brown parenchyma of the liver. These constitute the pancreas (Figure 2, *pancr*); the pancreas sends off a pancreatic duct on each side posteriorly. The two ducts unite into the short, sickle-shaped hepato-pancreatic duct (*d. hep. pancr*) which opens on the left side into the caecum.

Sections show that the efferent ducts of the liver open with their slightly polyhedral follicles in the anterior part of the collecting ducts of the pancreas. A median posterior indentation between the two halves of the pancreas is distinct.

529 The gland follicles in the anterior part of the pancreas are more densely arranged toward the outside than on the side facing the liver, where they are larger. This difference disappears posteriorly, where the pancreas becomes more sharply divided into halves by the deep indentation. The large ducts with their efferent canals extend to the margin of the indentation.

10. Genitalia

Male genitalia. The **testis** (Plate LXXXIV, Figure 4, *test*) is situated ventrally at the posterior end of the body and projects as far anteriorly as the stomach; the latter is situated dorsal to it. The testis is oval and transverse in young males but in the large male from Station 66 it is spherical, extends to the branchial hearts and is 12 mm wide; it borders dorsally on the stomach, the caecum and the liver. The genital artery and vein are clearly visible. The capsule of the testis (Plate LXXXVII, Figure 4, *caps*) is covered with chromatophores.

The **gonoducts** of young specimens form a small complex left of the testis but are not contiguous to it. They are covered dorsally by the left branchial hearts, the branchial vessels and the ureter. The whole complex is later displaced anteriorly so that the gill covers the distal part of Needham's pocket and the appendage of the prostate, while the penis (*pen*) projects freely as a diverticulum into the mantle cavity.

A more detailed examination of the gonoducts shows (Plate LXXXVII) that the vas deferens ("proximal vas deferens" of MARCHAND; Figures 5, 7, *v. def*) begins with a large mushroom-shaped ampulla (Figures 5, 7, *amp*). The vas deferens ends in a dome which opens broadly into the capsule of the testis. Numerous radial folds are present on the ampulla which is about 2 mm wide. The vas deferens is very short, shorter than in all Octopoda examined, and extends to the ampulla like the stalk of a mushroom

The **seminal vesicle** (*ves. sem*$^{1-3}$) is divided into 3 parts. The first part (*ves. sem*^{1}) may be mistaken for convolutions of the vas deferens. Closer examination shows, however, that the apparent convolutions are a great number of short, wide, glandular tubes which converge toward the lumen of the tube. This part is 4 mm long.

The 2nd part is horeshoe-shaped, about 6 mm long, with a swelling which projects inward (*ves. sem*^{2}). At the transition to the 3rd part (*ves. sem*^{3}) the walls become folded and form short glandular follicles; here opens also a whitish gland (Figure 7, *gl*) which consists of a few tubes, some of them long. The 3rd part, which is almost 12 mm long, has smooth walls and a longitudinal swelling along its whole course. Anteriorly, where it opens into the large prostate (Figure 5, *prost*), it narrows and has only longitudinal folds.

530 The **prostate** (accessory gland, "shunting gland" of MARCHAND) is 9 mm long from the opening of the duct (Figures 5, 6, *prost*). Its walls bear numerous dense follicles, which open in the wide lumen. The hood-shaped appendage of the prostate (appendix, *app*) is situated broadly on the beginning of the prostate and is 6 mm long to the opening of the vas deferens. This large part contains longitudinal folds which are curved toward Needham's pocket. Its lumen widens like a hernia toward the 3rd part of the seminal vesicle and narrows proximally to make place for a laterally situated aciniform gland (*gl. acc*), which resembles a sebaceous gland (Figure 9) and opens near the entrance of the spermatophore pocket. This hood-shaped part, which is 6 mm long, forms a common sinus for the prostate and Needham's pocket and corresponds to the appendix.

The **vas efferens** ("v. def. dist." of MARCHAND, 1907; Figure 5, *v. eff*) is wide and not sharply distinct from the appendix. It contains longitudinal folds which project markedly into the lumen and opens in about the anterior third of Needham's pocket which is still relatively short and narrow. Needham's pocket bears several folds and its posterior apex is slightly undulate and glandular.

Near the **penis** (*pen*) is a distinct ampulla-shaped dilatation (*x*) which passes into the penis through

a narrow canal (Figure 8). The penis has a well-developed diverticulum (*div. pen*); it is hatchet-shaped and has a dilated lumen without folds which is situated on Needham's pocket.

Topographical relationships of the gonoducts in the intact specimen. Examination from the ventral side shows that the 2nd and 3rd parts of the seminal vesicle partly cover the distal part of the prostate. Completely visible is the hood-shaped appendix with its transition into the dorsally directed Needham's pocket; also visible is the narrowed distal part, which passes into the penis and its diverticulum.

Observation from the inner side (dorsally) shows the ampulla and its opening, the nerve of the vas deferens and the 1st part of the seminal vesicle. The 1st and 2nd part of the seminal vesicle are thus almost completely covered by the *S*-shaped prostate, so that only the transition from the 2nd to the 3rd part with the gland is exposed. Also visible is the opening of the vas efferens in the exposed Needham's pocket; the ampulla-shaped distal swelling of Needham's pocket covers the appendix. The hammer-shaped penis and its diverticulum are also recognizable.

Comparing the gonoducts of the Bolitaenidae with those of the other Octopoda, they show the following characters. The very large ampulla has hardly an analogy. The 1st part of the seminal vesicle is short and the 3rd part long, as in all Octopoda. Their wide, hood-shaped prostate appendix is present
531 also in *Octopus* and in *Eledone.* A diverticulum of the penis of the same size is present in *Octopus*, while that of *Eledone* is small. Striking is their very short vas deferens; only in *Eledone* it is short, too.

11. Excretory organs

My examination of the excretory system was restricted, on the whole, to external observations; these, moreover, showed only few differences from those described for *Eledone* and other Octopoda by Grobben (1884, p. 25) and others.

The renal sacs are kidney-shaped in ventral view. However, if they are removed, they show an obtuse-triangular form, due to the fact that the lateral lobe of each renal sac is directed dorsally and becomes visible only if the organ is spread out. Opening of the mantle cavity does not show the renal papilla, because the latter is entirely covered by the base of the gill. If the gill is folded aside, the chimney-shaped papilla, which is slightly striated by folds and widened at the base like a flask, becomes visible (Plate LXXXVII, Figure 4, *ur*). The papilla adheres closely to the renal sac, in front and slightly left of the pericardial gland. Examination of these conditions is difficult because of the dense chromatophores on the inner side of the renal sacs, especially around the pericardial gland. The pericardial gland is spherical and surrounded by a plug of tissue which considerably narrows the lumen surrounding the gland. It probably corresponds to the flask-shaped appendage of Grobben (p. 28). Sections show that this is not a gland but a gelatinous part that contains numerous dense tubular or meandering septa which are covered with thin muscle fibers. Past the cavity of the water canal, which I followed for some distance toward the testis, the plug is surrounded by pavement epithelium resembling that on the pericardial gland. The cells of the epithelium become cylindrical only at the border between the pericardial gland and the plug.

Amphitretidae HOYLE

by Professor Dr. J. THIELE (Berlin)

The characters of the family as given by Hoyle are the same as those of the single genus.

Amphitretus HOYLE

According to HOYLE, the main character of the genus is the fusion of the mantle with the funnel, so that the opening of the mantle is divided in the middle. Other important characters are the gelatinous
532 consistency of the integument, the wide interbrachial web, and the presence on the arms of a single row of small suckers which are separated by intervals in the larger proximal half but are densely arranged and alternating in two rows in the distal part; cirri are absent. The characteristic eyes have been studied in detail by CHUN.

HOYLE considers *Amphitretus* as closely related to *Cirroteuthis*, mainly because of the large web and the single row of suckers on the arms, but also because of the extensive fusion of the mantle with the body. HOYLE writes: "In the delicacy and transparency of the tissues it also resembles *Bolitaena*, *Eledonella* and *Japetella*, but this may be an adaptation to pelagic life rather than a point indicating morphological relationship." IIJIMA and IKEDA stressed the absence of cartilages, fins and cirri as important differences from *Cirroteuthis* and noted some similarities with *Alloposus*, so that they consider the latter as its closest relative. The radula of *Alloposus mollis* VERRILL was illustrated by JOUBIN (*Résult. Camp. "Monaco"*, Vol. 9, Plate 5, Figure 11, 1895); it has a three-pronged middle plate, a rather small inner intermediate plate with a larger and a small tooth, and a larger outer intermediate plate with a simple tooth, as in *Polypus*. The jaws (Text Figure, p. 16) also show the usual characters.

I prepared the mouth parts of the specimen and find that they differ sharply from those of *Alloposus* but resemble closely those of the Bolitaenidae. The amphitretidae can thus be considered as most closely related to the Bolitaenidae, from which they differ mainly in the fusion between mantle and funnel and the size of the interbrachial web.

Amphitretus pelagicus HOYLE
(Plate XCI, Figures 6–10; Text Figures 64–66)

1885 *Amphitretus pelagicus* HOYLE, *Ann. Nat. Hist.*, Ser. 5, Vol. 15, p. 235.
1886 *Amphitretus pelagicus* HOYLE, *Rep. Voy. "Challenger"*, Vol. 16, p. 67, Plate 9, Figures 7–9.
1902 *Amphitretus pelagicus* IIJIMA and IKEDA, *Annot. Zool. Japon.*, Vol. 4, p. 85, Plate 2.

Locality: Station 102: 34°31.2′ S, 26°0.2′ E. Vertical net, 1,800 m. Agulhas Current.

The only specimen is illustrated without name in CHUN (*Tiefen des Weltmeeres*, 2nd ed., p. 535); but the plate in the work of the Japanese authors shows that the live animal has a different appearance,

due to the presence of a gelatinous envelope. The *Challenger* specimen was caught near the Kermadec Islands. Since it appears to occur also near Japan and has recently been found near South Africa too, this species seems to have a wide distribution. The present specimen is 55 mm long, i.e., not much larger than the *Challenger* specimen; the Japanese specimen is 190 mm long.

533 The jaws are very soft and flattened (Text Figure 64), resembling those in *Eledonella.* Examination of the cutting edge under the magnifying lens shows some thickened bands which extend like wings from the middle to the sides (Text Figure 65). The radula is rather short and wide, strongly narrowed anteriorly. The middle plate (Text Figure 66) has a broad base which is concave anteriorly and has a long, narrow, pointed tooth in the middle, flanked by 3 small teeth on each side. The inner intermediate plate is

a b

FIGURE 64. *Amphitretus.* a lower jaw; b upper jaw, surface view.

FIGURE 65. *Amphitretus.* Cutting edge of lower jaw.

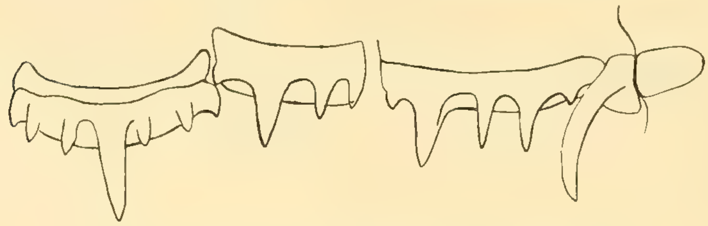

FIGURE 66. *Amphitretus.* Right half of tooth row of radula.

slightly narrower; it has a small inner tooth, followed by a large pointed tooth and two smaller lateral teeth. The outer intermediate plate is much wider; it also has a smaller inner tooth, a large tooth, two smaller teeth and a small denticle. The lateral plate is rather long, narrow and distinctly curved. The marginal plate is distinctly wider than long.

Description of the eye

by Professor C. Chun

(Reprinted from *Verh. Deutsch. Zoolog. Gesellsch.*, 1903, p. 88ff.)

The only specimen of *Amphitretus*, which we caught in the Agulhas Current, was slightly damaged but the eyes were intact. I therefore made longitudinal sections of the eye.

Seen from the outside, the eye (Plate XCI, Figure 8) is conical. The eyeball is 7 mm long and 4 mm wide; in the live animal its two lower thirds show a silvery-grey metallic sheen. The coloration extends to the lower margin of the epithelial body and does not cover the lens; the latter protrudes markedly and is covered by a thin iris. Eyeball and iris bear numerous orange chromatophores; an orange pigment is present also on the free margin of the iris and between the halves of the lens. The large optic ganglia, situated beneath the conical eyes which diverge outward, are clearly visible.

A longitudinal section perpendicular to the outer surface of the eye (i.e., more or less parallel

to a cross section of the body) is presented in Figure 9. The conical lengthening of the eyeball is caused by the unusual extend of the pigmented epithelium which is not covered by the retina. The
534 extremely large epithelial body (*c. epith.*) is steeply raised and situated on the slightly smaller lower half of the lens. The development of the epithelial body corresponds to that of the lens and especially of its upper half. Since the epithelial body forms the lens, the outer half of the epithelial body is as large as the inner half. The uniformly thin iris (*ir.*) extends from the posterior margin of the epithelial body, covering not only this but also the greater part of the anterior half of the lens. The lateral walls of the eyeball are very thin in the area of the pigmented epithelium (*ep. pg.*) but markedly thickened in the basal part. Here is situated the flattened retina (*ret.*), which extends slightly higher on the median side of the eyeball than on the outer side. The sections show not only the unusual thickness of the retina but also the undulate arrangement of its pigment. This condition seems to be due not so much to the preservation as to the formation of two areas of sharpest vision. One fovea is situated near the outer side of the eyeball (*fov.*), the other close to the inner side. However, the rods are not unusually long in the foveae. Other interesting details are the relatively large optic ganglion (Figure 9, *g. opt.*) and the dark position of the pigment of the retina. Langer's muscle could not be demonstrated. The layers of the retina are shown in Figure 10.

Vampyroteuthidae n. fam.

by Professor Dr. J. THIELE (Berlin)

Although CHUN (*Report on the Scientific Results of the "Michael Sars" North Atlantic Deep-Sea Expedition*, 1910, Vol. 3, Part 1, p. 22) recently placed the genus *Vampyroteuthis* in the family Cirroteuthidae, it seems preferable to create a separate family for this genus; this, because the radula of the Cirroteuthidae has disappeared, but in *Vampyroteuthis* it is present. *Vampyroteuthis*, therefore, cannot be placed in the Lioglossa LÜTKEN but belongs to the Trachyglossa. But *Vampyroteuthis* cannot be placed in any of the known families of the latter group: *Amphitretus* has a similar form of the body but shows other important differences. The large interbrachial web, and especially the cirri on the arms and the fins, show that—among the Trachyglossa—*Vampyroteuthis* is most closely related to the Cirroteuthidae. The form of the plates of its radula resembles that of *Argonauta*, but otherwise the latter differs markedly from *Vampyroteuthis*.

Vampyroteuthis infernalis CHUN
(Plates XC and XCI, Figures 1–5; Text Figures 67–70)

1903 *Vampyroteuthis infernalis* CHUN, *Aus den Tiefen des Weltmeeres*, 2nd ed., p. 88, Text Figure.
1914 *Vampyroteuthis infernalis* CHUN, *Rep. "Michael Sars" Exp.*, Vol. 3, Part 1, p. 22.

The best-preserved of the 3 specimens caught by the expedition is shown on Plate XC in the lateral,
535 dorsal and anterior aspect. This specimen was caught at Station 65 (1°56.7′S, 7°40.6′E) with a vertical net sunk to 1,200 m; the 2nd specimen was caught at Station 67 (5°6.2′S, 9°58.6′E), and the 3rd one at Station 85 (26°49.2′ S, 5°54′ E), with a vertical net sunk to 4,000 m in both cases.

The integument, where it is preserved, is black, the inner side of the interbrachial web is chocolate-brown, the cirri are whitish, the eyes purple.

The body is oblong-ovoid in dorsal view, with two slender fins below the middle of the body, which are situated closely to the dorsal surface.

The first illustration in the report shows a second pair of fins. This is due to error resulting from the damaged condition of the specimen: two shreds of skin were mistaken for fins. There is a marked transverse constriction above the eyes, at the beginning of the dorsal arms.

The mantle separates from the body behind the eyes and bulges markedly in the middle. The area covered by the mantle is not pigmented, except for a black, posteriorly widened median stripe above the intestine (Plate XCI, Figure 1). In one specimen, the mantle margin is attached on one side near the funnel, but the closing apparatus could not be detected.

The eyes are covered by a thin membrane with an opening almost 1 mm wide and have broad stalks (Plate XCI, Figures 4, 5; Text Figure 67). The proximal part of the eye forms a wide cup in which the eyeball is situated, with the lens directed obliquely anteriorly. The cup is 4 mm wide, the length from the base of the stalk to the outer side of the lens slightly less.

The dorsal arms are slightly longer than the ventral arms; their larger proximal half is connected by a web. Their anterior side is covered with paired, pointed cirri which are widely spaced in the middle

FIGURE 67. Eye of *Vampyroteuthis.*

FIGURE 68. Internal shell of *Vampyroteuthis.*

of the arms, especially on the dorsal arms; distally they gradually become denser and smaller, so that the apical cirri are barely recognizable. Suckers are absent in the proximal half of the arms. A few (3–6) small suckers form a single row on the distal half of each arm; they are wart-shaped, with a small opening in the middle.

Text Figure 68 shows the outline of the thin, hyaline membrane of the shell of the specimen from Station 85. It is pointed anteriorly, tapers posteriorly and has numerous concentric growth lines; it
536 is 9 mm long and 2.5 mm wide. The asymmetry is probably an individual irregularity.

Two flat, rounded, yellowish warts situated in the funnel not far from the anterior margin are probably a homologue of the funnel organ.

The ring-shaped lip which surrounds the pharynx shows 15 equally spaced indentations. The jaws have sharp points. The upper jaw is narrow, its outer part has a distinct edge, the inner part is short and rounded (Text Figure 69). The radula is well developed and of simple form (Text Figure 70). The middle plate is slightly concave anteriorly, rounded posteriorly, slightly longer than wide, with a short, sharp cutting edge. The next pair of plates is of similar form and size but slightly asymmetrical; the following plate is much larger and wider and has a stronger cutting edge which begins at the inner corner. The simple lateral plate is distinctly curved and fairly large; next to it is a narrow, squamous plate.

FIGURE 69. Upper jaw of *Vampyroteuthis.*

FIGURE 70. *Vampyroteuthis infernalis*; part of radula.

The head cartilages are rudimentary, the connective tissue soft and transparent. The intestine is brown. The pharynx is followed by a narrow, dark part which passes gradually into a widened, croplike, long, lighter-colored part; it then narrows again and opens into the stomach. The liver is large and yellowish. The aorta is visible above the esophagus.

The gills have 8 folded lamellae on each side. Behind the eyes are situated the olfactory organs in the form of small, laterally compressed, distally widened warts which are about 0.3 mm wide. There are a few whitish dots (luminous organs?) in the skin; in the specimen from Station 85 there is also a large yellowish wart in front of each fin; we failed to clarify its significance, due to the poor preservation.

The specimen shown in Plate XC is 37 mm long from the tips of the dorsal arms to the posterior end; the body is 16 mm long to the middle of the eyes, the head with the eyes is 13 mm wide.

The genus *Vampyroteuthis* can thus be characterized as follows: Octopoda with a wide interbrachial web, with two rows of cirri on the arms and with a few small suckers; body sac-shaped, with small fins; radula well developed, with simple, sharp cutting edges.

Cirroteuthidae KEFERSTEIN

by Professor Dr. J. THIELE (Berlin)

This family is characterized by two rows of cirri on the arms, a very wide interbrachial web, a pair of fins, and the absence of a radula. It contains the genera *Cirroteuthis* KEFERSTEIN, *Cirrothauma* CHUN and *Opisthoteuthis* VERRILL; *Vampyroteuthis* has to be excluded because it has a radula. *Cirroteuthis* is not represented in the collection of the Deep-Sea Expedition; as for *Cirrothauma*, only a single specimen exists, namely from the *Michael Sars* Expedition, and its description was again presented here. However, the Deep-Sea Expedition found two new species of *Opisthoteuthis* which are described below. Two species of this peculiar genus have been described: *O. agassizii* VERRILL (*Bull. Mus. Harvard Coll.*, Vol. 11, p. 113) from the North Atlantic and, later, also found by the *Michael Sars* Expedition (*Rep. Results "Michael Sars" Expedition*, Vol. 3, p. 21), and *O. depressa* IIJIMA and IKEDA (*Journ. Coll. Sci. Univers. Tokyo*, Vol. 8) the anatomy of which has been examined
537 in detail (cf. S. S. BERRY in: *Proc. Acad. Philadelphia*, 1912, p. 384). CHUN briefly mentions in his report that the genus was found in the Mentawei Basin and near the East African coast; he also illustrates an unnamed species (*Tiefen des Weltmeeres*, 2nd ed., p. 538).

Opisthoteuthis extensa n.sp.
(Plate XCIV, Figure 3; Plate XCV, Figure 2)

1903 *Opisthoteuthis* n.sp., CHUN, *Aus den Tiefen des Weltmeeres*, 2nd ed., p. 538, Text Figure.

Locality: Station 189: 0°57.5′ S, 99°51.1′ E. Trawl, 768 m. Mentawei Basin.

The only specimen is illustrated dorsally and ventrally. The species resembles *O. agassizii* but differs mainly in that the body is much wider and the middle part is more flattened.

The arms differ little in length: the dorsal arms are the longest, 12.5 mm, the second arms are about 11.5 mm long, the ventral arms 11 mm. As shown in the illustrations, all arms are markedly curved anteriorly, so that they appear to be arranged distinctly bilaterally symmetrical; the web is therefore broadly extended posteriorly, but it narrows distally in the anterior part and is markedly sinuate. The lower side of each arm bears a long row of small suckers; the inner (proximal) suckers become slightly larger up to the 5th sucker, while the outer suckers gradually decrease in size until they become so small that it is difficult to count them. To each side of the suckers is a row of small cirri. The color of the lower side is dark-brown in the middle, becoming lighter toward the margin.

The eyes are widely separated, with a distance of about 4.5 cm between the two openings. The fins are situated 1 cm from the posterior margin of the eyes and 3.5 cm from each other; they are narrow, pointed, 1.5 cm long and 1 cm wide. A cartilaginous rod which is 4 mm thick connects the fins. The upper side is darker in the middle than toward the margin. The network shown in the figure is comprised by small folds of the integument, perhaps caused by the preservation.

The funnel projects about 1 cm from the mantle opening; its length in the middle is 23 mm. The inner side of the funnel bears dorsally two *V*-shaped swellings which are situated closely together and apparently constitute the funnel organ.

The short anal papilla is situated in the anterior end of the funnel; closely behind it begins a narrow but strong band to the mantle. Between it and the left gill is the free end of the oviduct, which is 9 mm long and curved to the right. The gill consists of 6 adjacent swellings which consist of zigzag-shaped lamellae with short lateral branches.

538 ## *Opisthoteuthis medusiodes* n.sp.

(Plate XCIV, Figures 1, 2; Plate XCV, Figure 1)

Locality: Station 243: 6°39.1′ S, 39°30.8′ E. Trawl, 400 m. Near Dar es Salaam.

There are two specimens, one slightly larger than the other. The skin does not appear to be pigmented on the upper side, and as the illustrations do not show any pigmentation either, the animals were probably light-colored and transparent. Because of the absence of pigmentation and the medusa-like form of the body I named the species *medusoides*. The arms are more or less coiled toward the mouth and are connected by the web almost their whole length; when extended, they are only slightly curved, i.e., only the extreme tip—especially at the dorsal arms—is curved toward the middle of the dorsum.

The anterior side of the web is brown, the arms are light. The arms bear a single, dense row of small suckers; the suckers of one specimen were of about uniform size, those of the other specimen contained two markedly enlarged suckers (the 19th and 20th) at the beginning of the distal half of both ventral arms—probably a sign of hectocotylization. On each side of the suckers extends a row of cirri which usually alternate with the suckers; the base of the cirri is slightly retracted and often surrounded by a slightly raised, collarlike margin. The invaginated, funnel-shaped opening of the mouth is surrounded by a wide, circular swelling, covered with warts.

On the hemispherical posterior side of the body are the small, pointed fins; they are situated closely behind the eyes; further away from the eyes there is the mantle opening and the funnel which is 1 cm long in the middle. The funnel organ is apparently represented by a *V*-shaped swelling with the apex turned posteriorly.

The arms are 4.5 cm long; the distance between the fins is 24 mm, and that between the opening of the eyes 27.5 mm.

This species is apparently more closely related to the Japanese *O. depressa* than the two other species, but it differs from them more markedly than *O. depressa*, so that *O. medusoides* is the most aberrant species. It may have a different mode of life—unfortunately, this is unknown; at any rate, it is apparently less of a bottom-dwelling form than the other species; its almost gelatinous, transparent skin, in any case, is an important difference.

Cirrothauma Chun*

C. murrayi Chun

(Plates XCII and XCIII)

C. Chun, 1914, "Cephalopoda", *Rep. Scient. "Michael Sars" North Atlant. Deep-Sea Exp.*, 1910, Vol. III, Part 1, *Zool.*, p. 22ff.

Our treatment will be concluded with the description of a wonderful new type of Cirroteuthidae,

* This description is the German version of the report on *Cirrothauma* presented by Professor Chun in the *Rep. Scient. "Michael Sars" North Atlantic Deep-Sea Expedition*, 1910. It is reproduced here according to his wish and with the kind permission of Professor Hjort. Both plates are newly prepared. A. Brauer

539 perhaps one of the most valuable discoveries of the *Michael Sars* Expedition. The animal is completely gelatinous, semitransparent, and as delicate as a species of the lobed Ctenophora. Nevertheless, the specimen, which was preserved in formol, is in so good a condition that an accurate illustration can be given. Though the very delicate interbrachial web was torn, I give a photograph of the preserved specimen (Text Figure 71), in addition to the plates. The illustrations show that the completely gelatinous posterior end of the body ends in a pointed process and the mantle bears relatively large fins. The eyes are very small. The funnel is closely surrounded by the mantle slit and is long and slender. The arms are of about the same length and are connected by a web, except at the extreme tips. The measurements are as follows:

Length of body from posterior end to eyes	40 mm
Ventral length of mantle to funnel	37 mm
Length of each fin	39 mm
Length of 1st right arm	108 mm
Length of 2nd right arm	118 mm
Length of 3rd right arm	100 mm
Length of 4th right arm	110 mm
Width of eye	3 mm

540 The gelatinous tissue is delicately violet; only the mouth area and the proximal parts of the arms and web show the purple- to chocolate-brown tone which is characteristic for many deep-water forms. Because of its transparency, the nerves of the arms are recognizable along the entire length of the arms. The yellowish renal sacs show through anteriorly, while the branchial hearts are blackish. The stellate ganglion is visible as a small yellowish knob about 10 mm behind the eyes. Chromatophores are absent, except for a single large rhomboidal chromatophore on the ventral side, between the two fins.

I established the new genus *Cirrothauma* for this specimen mainly because of a character which is unique not only among the Cirroteuthidae but among all Octopoda: examination of the inner side of the arms shows tiny suckers, situated on long, plump, spindle-shaped gelatinous stalks. These stalks are 4–5 mm long in the middle of the arms and gradually become shorter toward the tips and proximally, where the stalks form plump conical tubercles until they finally disappear, so that the 6 proximal suckers of each arm have no stalks. Each of the arms bears 36 suckers. Figure 1 (Plate XCIII) shows the unusual condition of the arms. The stalked suckers have apparently lost their function—they are flattened, much smaller than the normal proximal suckers, and have no suction groove.

The spindle-shaped stalks of the suckers in the middle of the arm consist of gelatinous connective tissue on the surface of which are isolated longitudinal muscle cords which are distally dichotomously divided. Above these muscles there is an extremely delicate circular musculature; the interior of the stalks contains capillaries and, in the proximal third of each stalk, a whitish formation.

Sections through this inner body show that it consists of a shell with its dome directed distally. The opening of the shell is filled with a spherical cellular body which does not touch the margin of the shell. The shell is thickened toward the dome but becomes narrower toward the margin; it resembles a similar reflector occurring in the luminous organs of many Oegopsida. It consists of a cartilage-like substance with scattered nuclei which are surrounded by a light area. There is no pigmented envelope around the shell. The spherical cellular body contains numerous small, rounded nuclei but shows no distinct cell boundaries. Only on the proximal surface there are clusters of spherical cells that are more distinct.

It is with some reserve that I venture an interpretation of this structure. Without risking to advance a vague assumption, I can only say that the organ shows certain similarities with luminous

FIGURE 71. *Cirrothauma murrayi* CHUN, ventral view.

organs: The shell could correspond to the reflector, and the spherical cellular mass inside the opening could represent the luminous body.

The stalks of the suckers alternate with the slender, transparent cirri on each side of the suckers. The longest cirri are about 7 mm long. If this condition seems to be unique among the Cephalopoda,
541 there is yet another trait in *Cirrothauma* that presented a surprise: *Cirrothauma* **is the only blind cephalopod known.** The eyes, situated between the 2nd and 3rd arms, are only 3 mm wide. They do not protrude and have no lens. Deep inside the gelatinous substance, behind the eye, there is a second body; this led me into undertaking sections of the whole formation. The surroundings of the eye will not be described; they are illustrated in Plate XCIII which shows the isolated eye.

The eyes do not protrude but are completely embedded in the gelatinous tissue which forms a thick layer over the outer part of each eye.

The eyeball is almost spherical, only slightly flattened anteriorly, without pigment in the anterior

third but otherwise deep violet. The anterior border of the pigment is slightly irregular, extending a little farther on the ventral side. The eyeball is surrounded by a light-colored space (*a*) which comprises the outer chamber of the eye and is filled with water. It is completely closed: no external opening could be detected in the intact animal. The chamber projects slightly beyond the eyeball posteriorly and ends there in a ring-shaped thickening (*alb.*) which may perhaps be considered as a homologue of the white body. The sections show that the eyeball is completely closed, is very thin at its transparent anterior side, and only slightly thickened posteriorly in the pigmented area. The sections confirm the absence of a lens. The iris and ciliary body are also absent. The posterior side of the eyeball is surrounded by gelatinous tissue in which the thin optic nerve passes in the middle.

Behind the eyeball is situated a body (*s. ven.*) which is of about the same size and is also light-violet. Ventrally it is slightly displaced toward the main axis of the body. Posteriorly it is irregularly spherical and slightly concave. A large vein (*v. ophth.*), which may be homologous to the ophthalmic vein of the normal eye of Cephalopoda, extends to this body. As in *Bolitaena*, the ophthalmic vein forms a large sinus around the optic ganglion. However, sections show a very peculiar condition: the body is constituted by a large venous sac which is densely filled with blood cells. These cells are the cause of the dark tone of the formation—a tone that may easily be mistaken for that of an optic ganglion filled with small ganglion cells.

Deeper preparation shows the yellowish brain, from which extend 3 thin nerves toward the eyeball. The median nerve is the optic nerve (*opt.*). The optic nerve, though not completely reduced, is very thin in comparison with that of other Cephalopoda. It passes straight through the venous sinus,
542 without forming a swelling that could be interpreted as a ganglion pedunculi; between the venous sinus and the eyeball it widens into a small, knob-shaped swelling—perhaps the rudiment of the optic ganglion. Separate cords extend from here to the eyeball. The difference from the normal condition is striking. The optic ganglion, which is present in all Cephalopoda and shows a characteristic stratification of ganglionic cells, is reduced here to a slight thickening of the optic nerve behind the eyeball, without typical ganglionic cells. There are also two thin nerves which extend to the outer side of the eyeball, divide, and innervate the weakly-developed muscular lamellae in the gelatinous substance around the eye. The dorsal nerve corresponds to the superior ophthalmic nerve (*ophth. s.*), the ventral to the inferior ophthalmic nerve (*ophth. i.*).

Furthermore, there is a layer which may be considered as the retina (Figure 3). Examination of the pigmented half of the eyeball shows that the pigment consists of two layers. The inner layer forms a continuous thin cover on the eyeball, the outer layer appears at the periphery in the form of isolated flakes or scattered granules of pigment. The dark-violet coloration of the eyeball is caused mainly by the outer layer. Behind the inner layer of pigment are situated dense spherical nuclei which are arranged in two layers. These nuclei belong to the pigment cells and the cells of the retina. The marked reduction of the eyes is proved most distinctly by the condition of the rods. In all other Cephalopoda, the rods are densely arranged and glued together, so that they form a network in cross sections; here they are widely separated. They are very short and usually slightly pointed at their free end, so that they project above the layer of pigment like little flames.

This is so far-reaching a reduction of the eye that it is unprecedented in the Cephalopoda. We know deep-sea Cephalopoda with relatively small eyes, but the structure of the eye is never affected by this reduction. In addition to the absence of the dioptric apparatus, i.e., the lens and the ciliary body which secretes it, there is a far-reaching reduction of the optic nerve that has no parallel in other Cephalopoda. The ganglion pedunculi and the optic ganglion are absent, and the white body, which I consider to be constituted by the ring-shaped thickening (*alb.*), has also become rudimentary.

The most important layer of the retina, the layer of rods, also shows marked reduction. All these details confirm that *Cirrothauma* is the only blind cephalopod known. The eye is much more markedly reduced than in some blind vertebrates. Whether this reduction of the eye is correlated with the formation of luminous organs in the gelatinous stalks will have to be determined if and when a live specimen of this amazing form will become available and if it can be proved that the structures here mentioned are indeed phosphorescent.

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